NATURAL HISTORY OF *CERION* VIII: LITTLE BAHAMA BANK—A REVISION BASED ON GENETICS, MORPHOMETRICS, AND GEOGRAPHIC DISTRIBUTION*

STEPHEN JAY GOULD[1]

DAVID S. WOODRUFF[2]

Abstract. Close to a dozen names are now available to describe variation in *Cerion* on the islands of Little Bahama Bank. These names, plotted in the supposed areas of their occurrence, form the "crazy-quilt" distribution pattern, traditionally, associated with *Cerion* and ascribed to haphazard transport by hurricanes. We, on the other hand, find remarkably stable patterns in *Cerion* throughout the northern Bahamas. More than 200 "species" can be reduced to a single, unerringly predictable distribution and interaction of two imperfectly separated entities: a ribby morphotype associated with coasts that abut the edges of the Pleistocene banks, and a mottled morphotype from interior areas and coasts adjacent to bank interiors. We find the same distribution throughout Little Bahama Bank and reduce the current taxonomy to two semispecies: *C. bendalli* Pilsbry and Vanatta (the mottled morphotype) and *C. abacoense* Pilsbry and Vanatta (the ribby morphotype). The distribution of these semispecies maps the edges and interiors of Pleistocene banks, as described above; the morphological differences make sense in adaptive terms; wherever the taxa meet (at the junction of bank-edge and bank-interior coasts), they hybridize in narrow zones that exhibit characteristic morphometric and genetic patterns. We intend to use this combined morphometric and genetic study as a model for our biological revision of the entire genus.

We measured 20 characters in samples of 20 shells (when available) in each of 52 samples spanning the range of phenotypes and their geographic distribution in Little Bahama Bank cerions. Three factor axes encompass nearly all information (96.3 per cent) in the matrix of mean sample vectors; two axes account for 88 per cent. Ribby and mottled samples from Abaco sort unambiguously on the first two axes; the third axis distinguishes mottled samples from Grand Bahama by their characteristic covariance (high narrow shells with small and numerous whorls). All samples, defined as hybrids by their geographic position in zones of interaction (not by their morphology), have intermediate projections on the first two axes and plot in the intermediate phenetic field between them on a triangular diagram; samples of the hybrid zone at Rocky Point plot in perfect geographical order. Patterns within morphotypes are equally smooth and simple. Trend surface analysis displays the even variation in size (a multivariate compound of all measures) for mottled samples throughout Grand Bahama, the previous basis for three discrete "species"; minor, but consistent, differences characterize slightly isolated regions on Abaco—samples at Treasure Cay, for example. Samples from areas of interaction are intermediate in phenotype between ribby and mottled "parental" populations. At Rocky Point, the very narrow (less than 1 km.) hybrid zone displays continuous transition in mean phenotype with no increase in variability within samples.

A study of allozyme variation at 28 loci (6 variable and scorable) for the same samples yields very little concordance between biochemical data and patterns of variation in shell phenotypes. *Cerion*, though facultatively hermaphroditic, are outcrossing and moderately variable for structural genes surveyed (polymorphic loci per population, 20–36 percent; average heterozygosity per individual, 5–12 percent). All samples are markedly similar. Nei's I for 820 pairwise comparisons ranges only from 0.9451 to 0.9999 (average of 0.9849); no "marker" gene characterizes any region or morphotype—though characteristic frequencies of variable alleles clearly separate Grand Bahamian from Abaconian populations in a statisti-

[1] Museum of Comparative Zoology, Harvard University, Cambridge, Mass. 02138.

[2] Department of Biological Sciences, Purdue University, West Lafayette, Indiana 47907.

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cal manner. The genetic analysis of hybrid samples affirms our decision to treat the Little Bahama Bank cerions as two semispecies, rather than as geographic variation in a single entity. Although we find no increased variation in shell phenotypes, hybrid *Cerion* are significantly more variable genically (both within and among samples) than animals collected elsewhere. They are also polymorphic for alleles not found in either adjacent "parental" population.

I. INTRODUCTION

The current taxonomy of the Little Bahama Bank cerions is a microcosm of the problems that beset this entire fascinating genus, with its 600-odd named taxa (Clench, 1957; Mayr and Rosen, 1956). Little Bahama Bank was spared from visits by the most exuberant conchological splitters, but even its conservative monographers (Clench, 1938, for example) followed the hallowed tradition of naming every distinctive allopatric morphology. Seven species are now recognized for the islands of Little Bahama Bank.

A taxonomic scheme is not merely a neutral description of diversity; it is, as Mayr (1976) has emphasized, a theory of resemblances. And, like all theory, it channels thought along prescribed lines. In *Cerion*, the geographic mapping of described taxa yields a "crazy-quilt" (Mayr and Rosen, 1956) of disordered distribution. Published reports and museum specimens show this pattern for the seven taxa of the Little Bahama Bank (Fig. 1). All leading students of *Cerion* have invoked the vagaries of hurricane transport as an explanation for this incoherence (Maynard, 1919; Bartsch, 1920, p. 53; Clench, 1957; Mayr and Rosen, 1956). Yet if the taxonomy is incorrect—if these "species" are only local demes of persistent and widespread biological species—then this biogeographic postulate falls.

The few scientists who approached *Cerion* with the integrative goals of modern evolutionary biology have realized that something in the state of its systematics must be very rotten (Clench, 1957; Mayr, 1963; see also Plate, 1906 and 1907 for similar insights from a non-Darwinian evolutionary perspective). As a primary though generally unrecorded fact, no unambiguous case of sympatry has ever been reported among *Cerion*'s 600-odd taxa. The two most probable cases are both in doubt. Mayr (1963, p. 398) reported two species from one of his Cuban localities, but his specimens (S. J. Gould, personal observations) include a few clear intermediates. Bartsch (1920) reported no hybridization between two "species" from Andros Island transplanted to the same locality in the Florida Keys. But he later came to question his own observation (Bartsch, 1931, p. 373). In our own field work, extending over five years and as many major islands, morphotypes ("species" of previous authors) hybridize freely at their zones of contact, no matter how distinct their morphologies—and some of the zones on Long Island mark the smooth mixture of the most distinctly different morphologies within the genus (e.g., smooth, squat "*C. malonei*," with a long, triangular member of the peculiar subgenus *C.* (*Umbonis*); see Gould, Woodruff, and Martin, 1974, Fig. 1, upper row, specimens 3 and 4). Moreover, we have detected very little genetic difference among animals of divergent shell morphology (Gould, et al., 1974, Woodruff, 1975a,b). *Cerion* seems to possess a remarkable capacity (among animals) for developing localized, highly distinct morphologies without attendant reproductive isolation from other demes.

We wish to emphasize that our quest for a revised taxonomy is not motivated by any abstract desire for tidiness or simplification. Rather, a more adequate nomenclature both arises from and potentially leads to a better evolutionary understanding of *Cerion*'s unusual biology. A well-revised taxonomy is both a precondition and a promise.

We began our work in 1972 in the basic tradition of evolutionary natural history. We wished, first of all, to study selected islands in detail and, to map the distribution of morphological variation, hoping to find

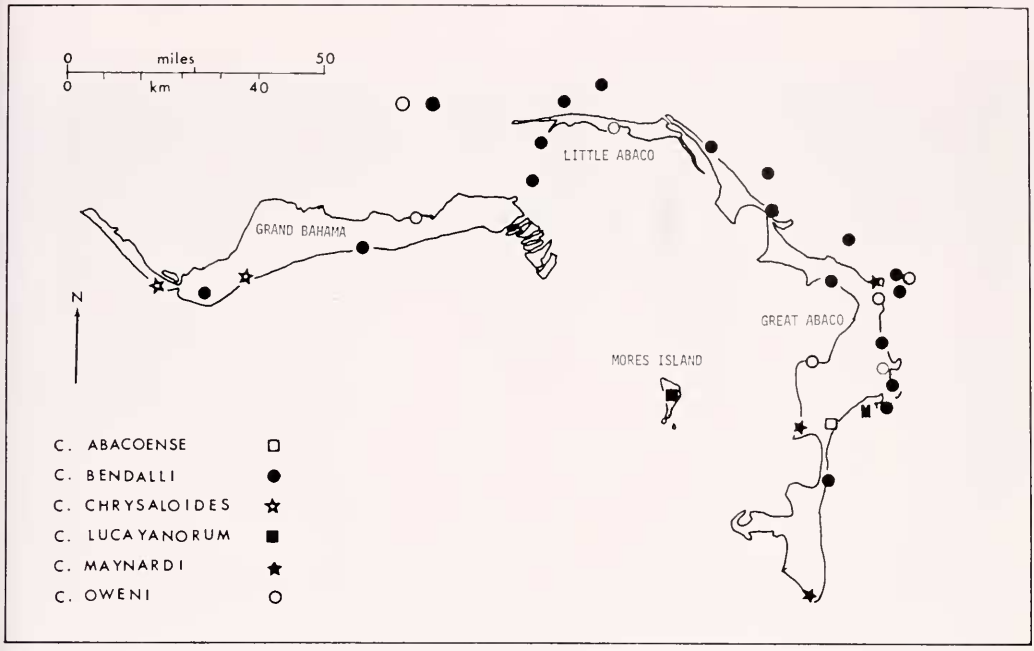

Figure 1. Distribution of *Cerion* on Little Bahama Bank as recognized taxonomically at the time this study was initiated. M marks Duck Cay, suspected by Clench as being the type locality of *C. milleri*. Pilsbry and Vanatta did not specify a locality for *C. abacoense* (beyond simply "Abaco" itself); we have placed it on the only part of Abaco where shells of its morphology occur.

some correlation with local environment. We also wanted to record everything we could observe about the virtually unknown basic biology of these snails (feeding habits, predators, etc.). Beyond this, we decided to apply a dual strategy of genetic and morphometric study of the same animals (as fruitfully applied, for example, by Soulé, 1976 and Johnston, 1975). Consequently, we collected large samples at many localities—either by gathering all the adult specimens we could find in about 30 minutes, or, in areas of high abundance, by recovering 100–200 specimens within an area of less than 100 m^2. Our genetic methods are described in Woodruff, 1975b; our morphometric approaches in Gould et al., 1974.

In our first report (Gould, Woodruff, and Martin, 1974), we showed that a local set of populations on Abaco Island, clearly distinct enough morphologically to win specific designation by all previous criteria, could only be ranked as a well-marked geographic variant within the only taxon inhabiting its general area. We now extend this approach to consider the entire *Cerion* fauna of Little Bahama Bank (Fig. 2).

II. GEOGRAPHIC DISTRIBUTION AND TAXONOMIC SIMPLIFICATION

Of the two major platforms that include most of the Bahama Islands, Little Bahama Bank is the smaller and more northerly. It includes (Fig. 3) the two major land masses of Abaco and associated islands on the northeast and eastern part of the bank, and Grand Bahama on the southwest and south. In contrast with Great Bahama Bank (6 major islands, hundreds of minor ones and about 250 recorded species of *Cerion*), it represents a tractable area for the study of *Cerion* over a broad and distinct portion of its range.

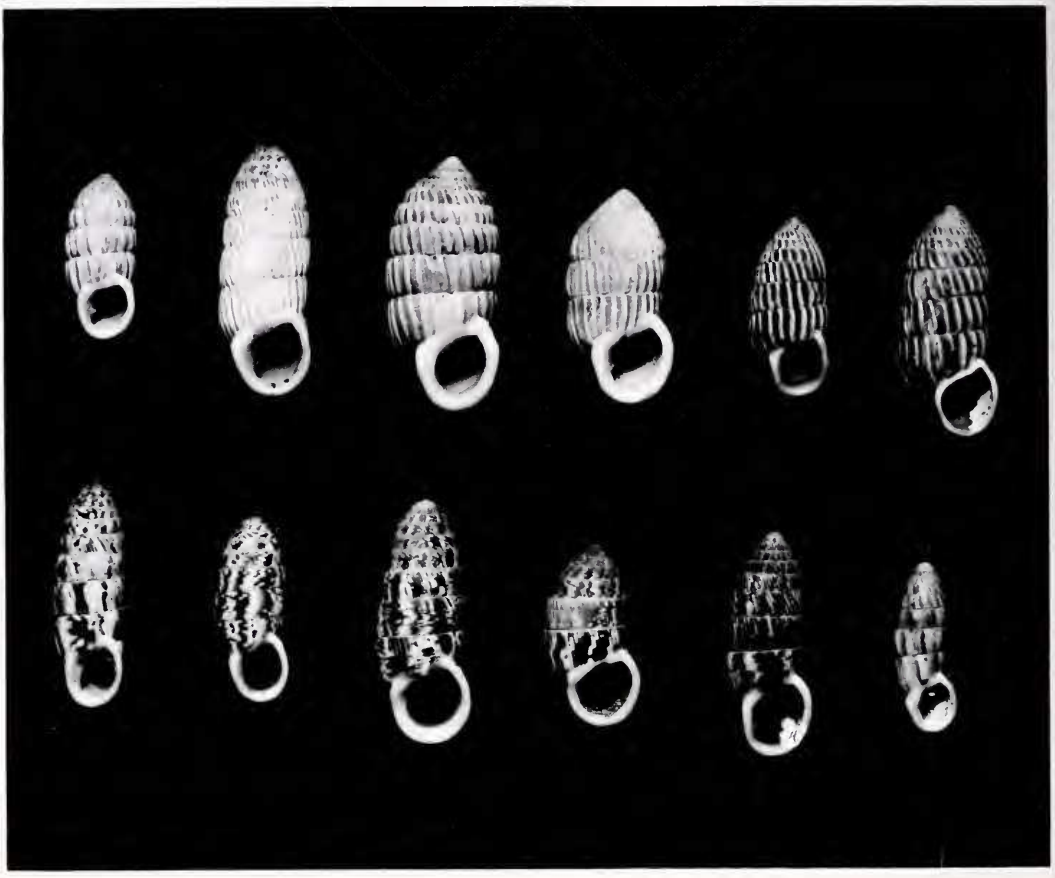

Figure 2. Representative specimens displaying the range of variation within the two morphotypes of the Northern Bahamas. Top: ribby morphotype. Bottom: mottled morphotype. Conventional taxonomy as follows: Top row, left to right: *C. chrysaloides*, Grand Bahama; *C. lucayanorum*, Mores Island (holotype); *C. maynardi*, southern end of Abaco, locality 250; *C. abacoense*, southeastern shore, Abaco, locality 254; *C. glans coryi* from western end of New Providence Island; *C. salinaria*, Salt Cay north of New Providence (holotype). Bottom row, from left to right: *C. bendalli*, Grand Bahama, locality 200; *C. bendalli*, Abaco locality 228; *C. bendalli*, western tip of Great Abaco, locality 217; shell that could be assigned to any one of 10–15 species, Culbert's Point, New Providence Island, locality 267; shell that could be assigned to any one of 10–15 species, central New Providence, locality 275; holotype of *C. degeneri* from New Providence.

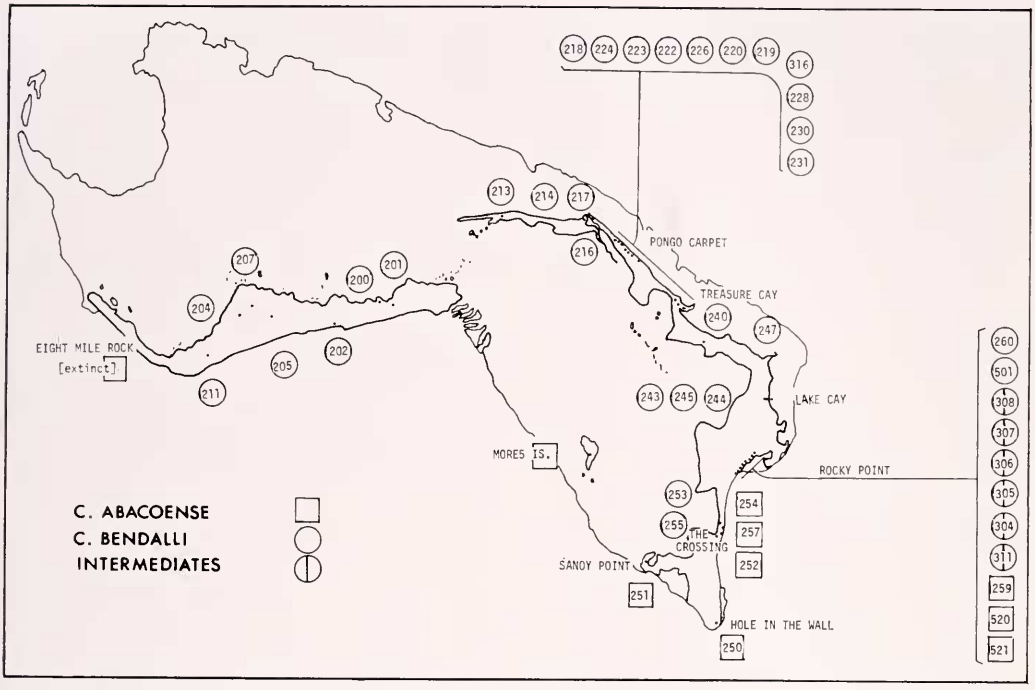

Figure 3. Distribution of *Cerion* on Little Bahama Bank revised in accordance with this study. Numbers refer to the authors' field localities and samples (see appendix). The edge of the bank is indicated. For details of the area of interaction on Great Abaco, see Figure 5.

Both previous monographers of Little Bahama Bank *Cerion* recognized that its several species could be allocated to two groups within the subgenus *C.* (*Strophiops*) (Pilsbry, 1902; Clench, 1938). Beyond this basic statement, the literature contains nothing of an explanatory or integrative nature. We have only a list of localities and taxa.

The two groups are distinct in morphology. Shells of the "ribby" morphotype are white or weakly mottled, relatively wide, and cylindrical with a fairly sharp break between a triangular apex and parallel-sided later whorls, strongly recurved aperture with thick lip, and a complete covering of strong, often widely spaced ribs (Fig. 2)—in short, a lightly colored, heavy and ribby shell. Shells of the "mottled" morphotype are strongly colored with irregular, brownish mottling, generally narrow with a more rounded apex passing smoothly to more barrel-shaped later whorls, apertures either thickly or thinly lipped depending upon the habitat (though never so thickly lipped as the ribby morphotype), with a shell surface either smooth or covered with fine ribs (Fig. 2)—in short, a mottled, light and relatively smooth shell.

We use the archaic term "morphotype" to describe these basic features because we find the same contrast—and the same correlation with geographic position and habitat—on island after island in the northern Bahamas. We have no reason to assert homology and transport among islands, though this has been the unstated assumption of all previous work. It is just as likely, we believe, that these basic morphologies are developed in situ, again and again, as adaptive responses to recurring habitats. On each island, the ribby and mottled

morphotypes interbreed in zones of contact; yet all the zones display features (varying from island to island) suggesting that at least a minor amount of genetic differentiation has occurred. They are imperfectly separated forms, perhaps best designated as semispecies, if conventional categories must be applied. (The biological species concept breaks down for an animal like *Cerion* with such amazing morphological diversity accompanied by, at best, imperfect reproductive isolation. We can scarcely recognize but a single species for a pattern of discrete and coherent morphological variation unexcelled among genera of land snails. Yet we cannot identify taxa by lack of interbreeding in sympatry.) We envisage a basic genetic system, common to all *Cerion* and including the potential to develop any one of a set of basic morphotypes. The morphotypes are alternative pathways of development that can be evoked from a common genotype by mechanisms of regulation utterly unknown to us. Once evoked, however, these morphotypes can become relatively stable within local areas. The basic features of any morphotype do not form a labile ecophenotype, easily altered by rearing in different conditions (Bartsch's transplants of Bahamian, Cuban, Puerto Rican, and Curaçao cerions all bred true to type for at least two generations on the Florida Keys and Dry Tortugas —Bartsch, 1920).

We believe that a modern taxonomy of the Little Bahama Bank cerions can do no more than recognize the two morphotypes as imperfectly separated semispecies. We base this conclusion on three sets of observations: consistent geographic distribution of the morphotypes, adaptive correlations with habitat, and patterns of interaction in zones of contact.

1. Geographic distribution. Among the myths that surround Cerion, none has been more persistent than the claim that it is a halophilic species restricted to coastal areas. All previously reported records for both ribby and mottled morphotypes are from localities within about 100 m of the sea. Yet we have found that the mottled morphotype ranges right across these low islands, penetrating the middle of the Grand Bahamian pine forest and the middle of the once forested area of Abaco. At locality 204 (see Fig. 3), 10 km from the nearest coast we found mottled *Cerion* at very low densities ($< 0.1/m^2$) in the shrubs and grass on the forest floor. Beneath one slab of aeolianite, however, we discovered an aggregation of more than 50 adults. Only in open, disturbed areas in the forest (locs. 205, 207) did we find *Cerion* in abundance (approx. $1/m^2$), and, even then, not in numbers typical of coastal populations where densities greater than $10/m^2$ are common. These sparse and patchy interior populations undoubtedly escaped the notice of early collectors, whose activities were usually restricted to a few minutes walk from the point where they beached their dinghies. W. J. Clench (1938), the most careful collector of *Cerion* found some interior specimens, but did not appreciate the generality of their occurrence.

In contrast to our discovery that the mottled morphotype ranges far from present day coasts, the ribby morphotype is restricted to within 200 m of the coast. Furthermore, and most importantly, it is restricted to coastal areas adjacent to the edge of the island bank (Fig. 3, for example). In contrast, the mottled morphotype occurs along coasts that do not border the island bank. If we designate the ribby morphotype as having a "bank edge" distribution, then the mottled morphotypes are found in "bank interior" situations. The mottled shells may represent an inland or bank interior morphotype evolved for geographic or ecological conditions prevailing during Pleistocene hypothermal periods when the sea level was much lower than it is today. If this hypothesis is correct, then the mottled morphotype has been living in coastal situations (along the northern coast of Grand Bahama and the western coast of Abaco) for less than 6,000 years. In contrast to the

traditions of *Cerion* study, and for reasons presented herein, we believe that current distributions may be highly persistent. The preference for fluid, haphazard distributions proposed by earlier workers (illustrated in Fig. 1) arises from a taxonomy that we will show to be fundamentally incorrect.

Distribution patterns based on the revisions in this paper are shown in Figure 3. The generally coherent pattern of bank edge vs. bank interior distribution found in these two taxa is one of our most important findings: it permits us to predict the distribution of analogous morphotypes on the various islands of the Great Bahama Bank. On Andros, New Providence, Great Exuma, and Long Island, we have found that the mottled morphotype invariably lives on bank interior coasts and inland areas, while the ribby morphotype is restricted to bank-edge coasts. We expect eventually to show that more than 200 "species" of Bahamian *Cerion* only represent the distribution of these two morphotypes and their interaction.

The consistent differences in distribution provide, in themselves, a strong argument for regarding the two morphotypes as partly distinct, biological taxa. They live on different kinds of coasts and react differently to inland conditions. Were it not for their patterns of interaction (see below), we might regard this strong correlation of form with habitat and geography as an aspect of normal geographic variation within a single taxon (perhaps purely phenotypic), rather than as the adaptations of imperfectly separated entities.

2. Adaptation of form to habitat. For all the effort devoted to taxonomy (more than 2,000 printed pages), no previous workers have directly studied the adaptive nature of form in *Cerion*. Nonetheless, the persistent correlation of form and habitat suggests that the morphotypes have been selected for survival value. Accordingly, we have initiated a series of experiments designed to establish some of the physical correlates of the various morphologies. Looking first for the possible adaptive significance of shell pigmentation, we contrasted the white shells of the ribby morphotype with those of the mottled morphotype. John Quensen, working in Woodruff's laboratory, found that in direct sunlight the interior of a mottled shell averages 1°C warmer than the interior of an unpigmented shell. It may well be that the ribby shells, characteristic of exposed bank-edge situations, are protected from overheating by the lack of shell pigmentation. Such an ecological correlation between shell color and body temperature has been found in other land snails (Rensch, 1932; Schmidt-Nielson et al., 1971; Yom-Tov, 1971; Heath, 1975). It is also possible that shell pigmentation plays a role in predator avoidance. The mottled shells are initially hard to find, as they hang from bush stems and on blades of grass in the dabbled sunlight and shadow (a clear case of disruptive coloration to our eyes) (Fig. 4). In contrast, the white shells of the ribby morphotype are fairly conspicuous on the stems and leaves of bushes and other plants. Only when they descend to the ground in rocky areas is their coloration at all cryptic. In a second investigation, Quensen has examined Vermeij's (1975) suggestion that sculpturing (ribbing) is a defensive adaptation in snails since it confines the predator's crushing force to the thickest part of the shell. Quensen's preliminary results indicate that, in *Cerion*, overall shell size is more important than ribbing in determining the strength of the shell. Approximately 80 percent of a shell's ability to resist fracture is attributable to shell weight and shell height; interrib shell thickness is more significant than shell thickness at a rib or ribbing density. This does not mean that ribs are unimportant in *Cerion*'s defense, but only that they do not protect the animal from compression applied generally along the sides of the shell. While the identity of *Cerion*'s key predators remains unknown, Woodruff's detailed population studies on Abaco and elsewhere implicate land crabs,

Figure 4. Cryptic nature of mottled coloration. When sunlight is filtering through bushes, the mottled shells are very hard to see (at least for us). Photo taken by J. Martin on northeast coast of Great Abaco.

rats, and possibly a bird. The results of these studies will be reported elsewhere (Woodruff and Quensen, in prep.).

3. Patterns of interaction. Populations of the ribby morphotype once inhabited the bank edge at Eight Mile Rock on the southwest Coast of Grand Bahama (Plate, 1907). In 1936, Clench and Greenway searched extensively for this form in the area where Millspaugh originally collected it. After two weeks they found only a single dead shell on the eastern side of Hawksbill Creek. Clench (1938) concluded that the hurricane of 1935 may have destroyed this colony, as it did a great deal of damage along the entire south coast of the island. In 1963 and 1964, small samples of ribby shells were again found at Freeport and Smith's Point (specimens in the Museum of Comparative Zoology). In September 1972, we spent several days searching the south coast of the island, from Freeport to West End; no *Cerion* were found. This is the only case we know in which a morphotype has apparently become extinct on an entire island.

On Abaco, however, we need only a map of bank edges to predict exactly where the contacts between ribby and mottled morphotypes should occur. The village of Sandy Point (Fig. 5) marks the coastal transition from bank edge to bank interior; here we collected a sample of intermediate morphology. The ribby morphotype inhabits the coast south of Sandy Point, around the southern tip of the island, up to the narrow area known as The Crossing (Fig. 5). Here, the second contact occurs as the interior, mottled populations are squeezed into close contact with ribby animals on the eastern shore. We observed no interactions; a narrow hill, running parallel to the coast, seems to separate the morphotypes com-

pletely. Yet there must be some "leakage" across the hill, for morphometric analysis (see below) demonstrates the intermediate nature of apparently mottled shells at this locality. According to the map, we must predict an interaction around Cherokee Harbor (Fig. 5), for here the coast again switches from bank edge to bank interior. Here, indeed, is the third and by far the most interesting interaction. Ribby populations, extending from the south, encounter mottled populations from the north in an apparently smooth, but local hybrid zone. We shall analyze this zone in detail in the following sections on morphometrics and genetics (see also Woodruff and Gould, in press) since it holds the key to our interpretation of these two taxa.

The current taxonomy of Abaco cerions recognizes seven taxa within these two morphotypes. Ribby populations have been allocated to four species:

1. *Cerion abacoense* Pilsbry and Vanatta, 1895, p. 209. The type specimen (Acad. Nat. Sci. Phila. No. 25337) and all associated museum material (M.C.Z., Harvard University, and Acad. Nat. Sci. Phila.) clearly indicate that this name applies to ribby populations from The Crossing, north to the hybrid zone. These shells are somewhat smaller, lighter with more though weaker ribs than southern samples. Pilsbry and Vanatta list their locality simply as "Abaco Island."

2. *Cerion maynardi* Pilsbry and Vanatta, 1895, p. 210. Again, listed only as "Abaco Island," but we have found this morphology only near Hole-in-the-Wall Light near South Point (southern tip of the island) where ribby shells are larger with very strong and sparse ribs.

3. *Cerion chrysaloides* Plate, 1907, p. 597. The extinct, bank-edge population collected by Millspaugh at Eight Mile Rock on the southwestern coast of Grand Bahama. Shells are considerably smaller than those of other ribby populations, but differ from them in no other evident way.

4. *Cerion lucayanorum* Clench, 1938. A longer and more slender shell with more numerous and finer ribs. From Mores Island (Fig. 3).

These populations are distinct in morphology one from the other. Indeed, all students of *Cerion* (including ourselves) agree that virtually every local population in this peculiar genus has its own recognizable form. (Disagreement centers only on appropriate taxonomic definition.) In this case, we cannot possibly justify any separation into species. We can barely distinguish the far more different ribby and smooth populations on the basis of their patterns of interaction. It is not likely that any reproductive barriers exist among local populations of the same morphotype. (Gould and Paull, 1977, have lumped within-morphotype variation for all cerions from Hispaniola to the Virgin Islands into a single species.) We therefore reject *C. maynardi*, *C. chrysaloides*, and *C. lucayanorum* as synonyms of the first-named form, *Cerion abacoense*. The ribby morphotype of Little Bahama Bank should bear this name, at least until we can determine whether it is homologous with populations of the ribby morphotype on islands of Great Bahama Bank.

At least two, and possibly three, names are available for populations of the mottled morphotype.* The rejected names for the ribby morphotype apply to geographically distinct subpopulations meriting subspecific rank, if we were inclined—as we decisively are not, lest *Cerion* maintain its burden of hundreds of names—to use this category. The "species" of the mottled morphotype, on the other hand, have no geographic definition; they are names

* Things could have been worse. Specimen labels in the Department of Mollusks, United States National Museum, include two additional names, apparently never published by Bartsch. These anagrams of the island—*C. mahaba* (U.S.N.M. No. 179439) and *C. hamaba* (U.S.N.M. No. 369715)—both apply to dwarfed forms of *C. bendalli* inhabiting the northern coast of Grand Bahama Island.

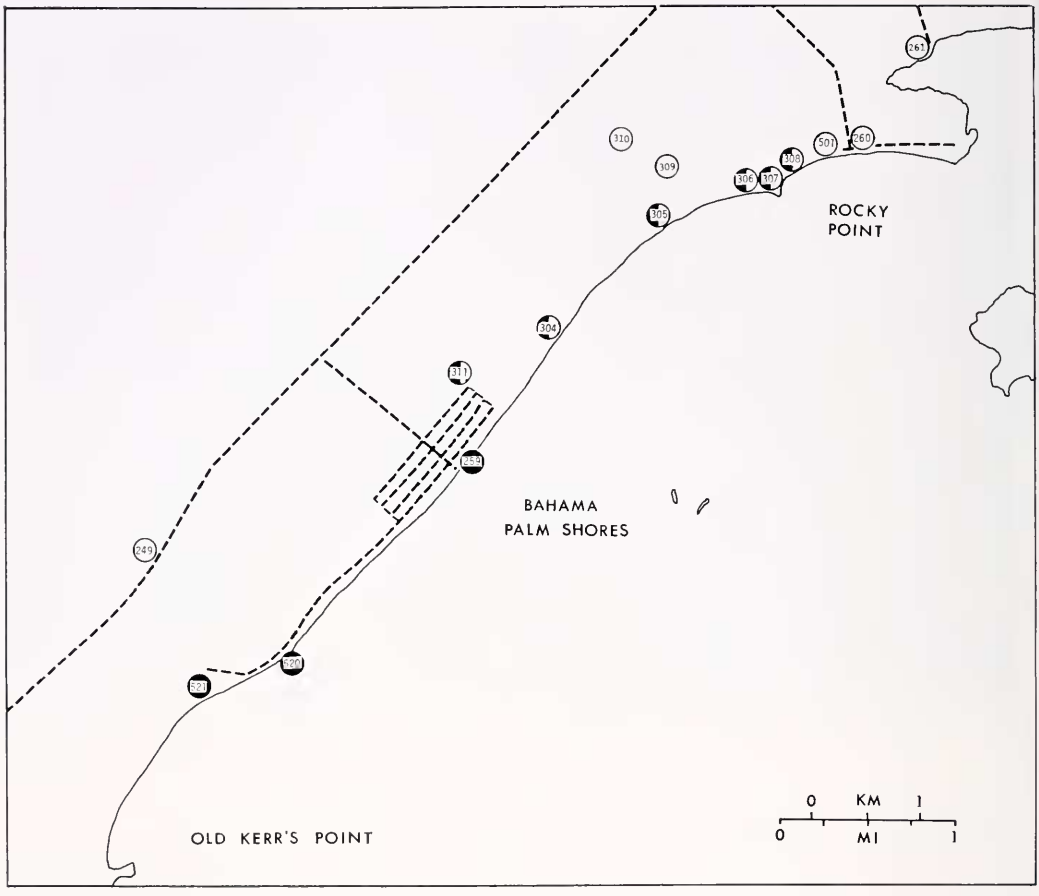

Figure 5a. Area of interaction between *C. bendalli* and *C. abacoense* on southern Great Abaco. Modal morphotype at each locality is indicated: *C. bendalli*, open circle; *C. abacoense*, closed circle; intermediates, half-closed circle.

for minor, recurrent differences in form throughout the range of mottled demes:

1. *Cerion bendalli* Pilsbry and Vanatta, 1896, p. 332. In an uncharacteristic act of lumping (overlumping, in our judgment!) Pilsbry and Vanatta originally defined *C. bendalli* as a subspecies of the ribby *C. abacoense*—though they wrote (1896, p. 333): "This form at first sight looks extremely different from *C. abacoense*, and as we have seen no intermediate examples, it may well prove to be a distinct species." In 1902, Pilsbry returned to his former consistency and elevated *C. bendalli* to specific rank. Pilsbry and Vanatta applied this name to samples of the mottled morphotype with fine ribs.

2. *Cerion oweni* Dall, 1905, p. 443. A name for smooth or very finely ribbed samples of the mottled morphotype; no other characters distinguish it from *C. bendalli*. Dall (1905) recognized three subspecies within *C. oweni* (*C. oweni incisum*, *C.o. vermiculum*, and *C.o. veticulatum*), but these have already been rejected by Clench (1938, p. 328).

3. *Cerion milleri* (Pfeiffer), 1867, p. 129. Pfeiffer applied this name to a small sample

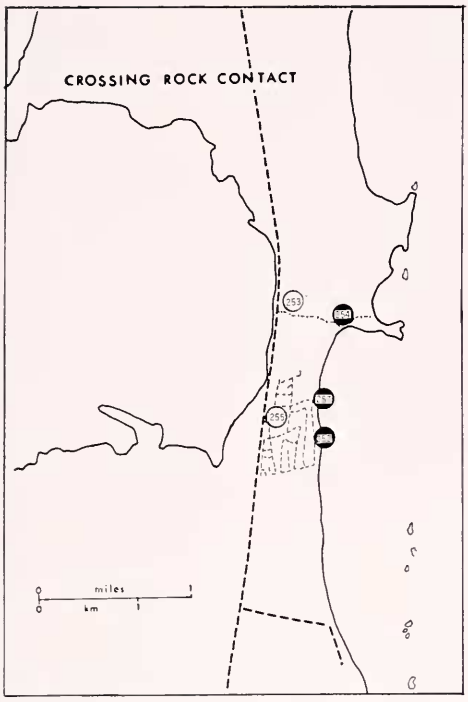

Figure 5b. Area of interaction between *C. bendalli* and *C. abacoense* on southern Great Abaco. Modal morphotype at each locality is indicated: *C. bendalli*, open circle; *C. abacoense*, closed circle; intermediates, half-closed circle.

of mottled shells from "Duck Cay, Exuma Group, Bahama Islands." But Clench (1935, p. 50) noted that the Exumas contain no Duck Cay, while an appropriate islet of this name sits in Cherokee Harbor, Abaco. He therefore supposed that *C. milleri* might be an Abaconian species. If Clench is correct, then *C. milleri*, as the oldest available name, should designate the mottled cerions of Little Bahama Bank. Yet we prefer to leave it in limbo, for we do not know how to verify Pfeiffer's locality; mottled shells are much of a muchness throughout the Bahamas, and occur throughout the Exumas.

We therefore reject *C. oweni* Dall (with its three subspecies) and *C. milleri* (Pfeiffer) and designate the mottled morphotype on Little Bahama Bank as *Cerion bendalli* Pilsbry and Vanatta, 1896.

III. MORPHOMETRICS OF CERION ON LITTLE BAHAMA BANK

A) *Introduction*

We were originally attracted to Cerion because it is such an ideal animal for morphometric study. Like most mollusks, it preserves a complete record of its ontogeny in an accretionary shell. Its particular advantages arise from two properties of growth: 1) The transition between embryonic shell and later accretionary growth is precisely marked by a discontinuity in ribbing and rate of expansion; we therefore obtain an unambiguous, biological criterion for numbering whorls; we take this discontinuity as the beginning of the 0'th whorl. This numbering permits us to define morphometric properties at a variety of standardized stages throughout growth. 2) As it reaches maturity, *Cerion* changes its direction of coiling and, finally, secretes a terminal adult aperture with an expanded and reflexed lip. We can therefore measure the traits of its definitive adult size. (Most mollusks have no stage of terminal growth; we can define neither the mean nor variance of adult characters because we cannot sort ontogenetic from static adult variation.) In *Cerion*, we can compare adult characters with corresponding traits at any stage of growth; in most mollusks, we can define neither set of measures unambiguously.

We have chosen a suite of variables that should measure all of the traits (except color) commonly used to erect taxa within *Cerion*. Our set also defines the major aspects of growth and covariation: size and shape of the embryonic shell, patterns of ribbing, size and shape of juvenile and preadult whorls, number of whorls, measures of final size, and characters of the adult umbilicus and aperture. Although our measures contain some inevitable redundancy, our previous studies clearly demonstrate at least five independent patterns of covariation among them (Gould et al., 1974; Gould and Paull, 1977).

Our measures follow the definition and

protocol of Gould et al. (1974, pp. 522–524) with the exception of 6 and the addition of 20 (used only as the numerator of ratio measure 18 in Gould et al., 1974; we have since determined that it includes interesting, independent information of its own):

1. width of the protoconch
2. width at the end of the fourth whorl
3. total number of whorls (with the termination of the protoconch taken as the 0'th whorl)
4. number of ribs on the fourth whorl
5. number of ribs on the sixth whorl
6. number of ribs in 50 micrometer units at the termination of the first whorl
7. length of the adult shell, apex to lower apertural tip
8. maximum width of the adult shell
9. height of the protoconch
10. total height of the shell at the end of the fourth whorl
11. height from the end of whorl 4 to the end of whorl 6
12. width of the umbilicus
13. width of the apertural lip at its widest point (measured parallel to the plane of the aperture
14. thickness of the apertural lip at its thickest point (measured perpendicular to the plane of the aperture)
15. height of the aperture
16. width of the aperture
17. protrusion of the aperture
18. tilt of the aperture
19. weight of the shell
20. distance from aperture to preceding suture: line EC of Gould et al., 1974, fig. 5, p. 523.

B) *The Basic Pattern*

We chose 52 samples, representing all taxa and habitats, and measured 20 shells from each sample when available—14 samples contain fewer shells, but only 5 of these have fewer than 15 specimens. Localities are listed in the appendix. Forty-eight samples are from our own field collections, 4 from the collection of the Department of Mollusks, Museum of Comparative Zoology, Harvard University [3 of the extinct ribby morphotype ("*C. chrysaloides*") from Grand Bahama, 1 of "*C. lucayanorum*" from Mores Island]. We are more than conventionally grateful to John Hevelin for spending half a year compiling one of the most scrupulously accurate data sets ever assembled in molluscan biometrics.

Many strategies are available for reducing a data set of 20 measurements on nearly 1000 specimens from 52 samples. We decided to treat each sample as a potentially random extract from a single statistical universe, rather than as a definite entity to be separated, if possible, from other groups. This decision—a methodological correlate of our belief that *Cerion* is a single entity with local inhomogeneities led to a factor-analytic model. We computed the mean vector for each sample (Table 1) and performed a Q-mode factor analysis of the 52 items using program CABFAC (Klovan and Imbrie, 1971). We included the following data transformations:

1. percent-range method of equalizing weights. The highest value of each variable receives a value of 100, the lowest becomes 0; others are scaled as a percentage of this range. This is not always (or even often) a desirable method for achieving equality of weights. Suppose, for example, that a trait varies narrowly and randomly among specimens. We would not want such variation to count as much as the wider range of another measure clearly adapted to variation in habitat. But, in this case, our values are well-determined means of samples, not the random error of individual specimens. A stable narrow range may be just as important as a wider one.

2. normalization of vectors. Each vector is rescaled to unit length before the extraction of eigenvalues. This transformation removes the explicit influence of variation in average shell size among samples. (However, the allometric correlates of size may still be expressed as shape.) We preferred to eliminate this explicit variation in size

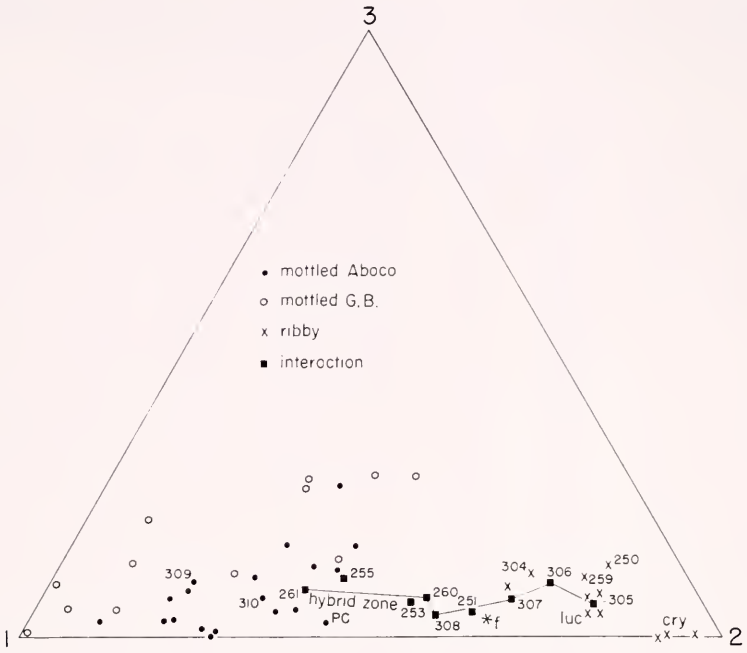

Figure 6. Position of mean vectors for all samples of Little Bahama Bank cerions. This is a triaxial plot of normalized factor loadings for a 3-axis, varimax solution in the Q-mode. These three axes explain 96.3 per cent of all information; the first two axes explain 88 per cent. Ribby and mottled morphotypes are well separated by the first two axes. Mottled samples from Grand Bahama Island have higher projections on the third axis. Closed circles are mottled samples from Abaco; open circles are mottled samples from Grand Bahama; crosses are ribby samples; squares represent samples defined by geography and ecology (not morphology) as inhabitants of zones of interaction between ribby and mottled populations (note their intermediate position in morphology as well); the star represents the single fossil sample from Abaco. The line connects samples of the hybrid zone at Rocky Point in geographical order. pc is the Pongo Carpet sample (mottled, partly convergent upon ribby); f is the fossil sample; cry are "*C. chrysaloides*" (the name applied to ribby samples on Grand Bahama); luc is "*C. lucayanorum*" (ribby sample from Mores Island). Other numbers refer to localities discussed in text.

because it can control so much covariance in a matrix (large shells have high values of almost all variables), and because all morphotypes and areas contain both large and small-shelled samples. We eliminate this pervasive control of size in order to see smaller but more stable influences more clearly. However, we also performed an analysis without normalization and obtained nearly identical results (see below).

Three axes encompass 96.3 per cent of the information in 52 samples; no subsequent axis reaches one per cent. We performed a varimax rotation and computed the factor loadings of all samples upon the three axes (in Q-mode analysis, samples are loadings). CABFAC normalizes the triaxial loadings to permit a plot as a triangular graph.

Figures 6–7 display a remarkable result. All the variation in Little Bahama Bank cerions, the basis of 7 species and a host of subsidiary distinctions, reduces to a matrix not far from rank 2! (Two varimax axes explain 88 per cent of all information.) And the foci of these axes are our two old friends—the ribby and mottled morphotypes in their "pure" form. All intermediate samples from zones of contact—and only these samples—plot in between. Moreover, the minor third axis has its own coherence, for all samples that load strongly upon it (with one excep-

TABLE 1. MATRIX OF MEANS (IN MM, G, OR COUNTS) FOR ALL SAMPLES TREATED BIOMETRICALLY IN THIS WORK. (CONVERTED FROM ORIGINAL DATA IN MICROMETER UNITS—VARIABLES 1, 9, 13, 14 MULTIPLY BY 18.0; VARIABLES 2, 10, 11, 12, 15, 16, 17, 20 MULTIPLY BY 8.0 FOR MICROMETER UNITS. ALL BIOMETRICAL WORK DONE IN MICROMETER UNITS. DATA IN THIS FORM AVAILABLE FROM AUTHORS.)

Sample Number	Location	Proto-conch width	4th whorl width	total whorls	4th ribs	6th ribs	1st ribs	height	width	Proto-conch height
92367	Grand Bahama:	2.74	7.79	7.50	21.33	19.67	6.83	22.77	9.57	1.26
247236	ribby	2.84	8.16	7.41	22.85	20.80	7.08	23.90	10.11	1.38
250620		2.78	8.23	7.33	23.47	21.67	7.63	23.21	9.96	1.39
212	Grand Bahama:	2.93	8.20	8.30	79.83	57.60	17.00	23.99	9.05	1.19
211	mottled	2.94	8.50	8.71	48.00	44.00	11.45	26.96	10.44	1.30
208		3.03	8.81	8.29	60.60	52.20	12.53	25.13	9.81	1.26
204A		3.29	9.65	9.20	53.83	47.78	12.58	32.09	11.86	1.39
204B		3.15	9.41	8.63	48.75	44.05	12.05	27.86	11.28	1.27
207		3.09	8.22	9.28	86.00	77.95	16.13	28.91	10.79	1.35
209		2.79	7.52	8.99	100.00	81.00	13.58	23.05	9.17	1.27
205		3.11	9.25	8.80	73.10	68.80	12.42	29.86	11.53	1.25
202		3.19	9.47	8.51	71.30	65.65	13.65	29.74	11.61	1.39
199		2.71	7.27	7.20	94.88	73.31	16.83	20.07	8.08	1.32
200		3.15	8.37	8.71	99.25	78.50	18.10	27.11	9.93	1.32
201		3.03	8.33	8.93	93.90	83.35	15.60	27.68	10.18	1.27
213	Little Abaco	3.22	9.36	8.70	85.55	75.55	15.78	31.27	11.06	1.32
214		3.13	9.14	8.38	100.85	86.65	17.93	28.05	10.58	1.22
216		3.04	8.81	8.17	93.70	73.05	17.85	26.15	10.08	1.29
217	Great Abaco	3.17	9.18	8.21	95.56	71.28	16.09	28.83	11.00	1.35
218		3.00	8.98	9.04	80.25	60.40	14.85	32.61	11.37	1.28
316		2.85	8.03	7.93	58.45	41.15	13.85	24.68	9.63	1.34
228		3.02	8.31	7.89	81.45	63.10	14.43	24.27	9.61	1.50
229		3.05	8.39	8.02	79.21	67.33	15.97	25.31	9.87	1.47
230		3.00	8.08	8.43	95.95	85.21	18.23	26.08	9.82	1.41
231		3.05	8.74	8.85	78.80	61.10	14.82	30.49	11.47	1.48
233		3.42	9.06	9.25	96.00	76.00	16.50	31.10	11.20	1.54
240		3.10	8.89	8.71	80.65	62.65	15.72	29.56	10.83	1.27
247		3.18	8.81	7.88	103.20	75.35	17.30	25.26	10.15	1.26
246		3.02	8.38	8.42	47.68	40.00	10.58	25.92	9.93	1.55
243		3.29	8.97	8.53	100.00	84.06	17.91	27.08	10.61	1.31
245		3.38	9.66	8.23	95.70	79.35	17.05	28.14	11.00	1.37
244		3.25	9.17	7.79	97.80	74.85	14.90	25.23	10.24	1.24
261		3.21	9.73	8.55	94.71	78.57	15.36	30.26	10.99	1.33
260		3.13	9.40	7.84	58.85	49.45	12.63	26.73	11.13	1.31
308		3.08	9.23	7.68	53.50	45.65	12.90	25.76	10.96	1.31
307		3.02	9.38	7.84	46.65	41.10	11.40	26.97	11.39	1.35
306		3.17	9.95	7.93	44.10	38.90	10.95	28.68	12.18	1.35
310		3.39	10.53	8.13	95.82	74.90	15.78	27.60	11.82	1.39
309		3.38	9.78	8.12	98.33	89.56	16.70	28.88	11.38	1.37
305		3.12	9.95	7.76	39.80	34.65	10.53	28.83	12.15	1.37
304		3.11	9.82	8.08	44.40	39.90	11.43	29.52	12.30	1.33
311		3.04	9.51	7.94	44.20	39.15	10.95	27.52	11.45	1.35
259		3.08	9.68	8.22	38.80	34.45	9.95	31.37	12.83	1.36
249		3.63	10.35	9.46	82.05	74.95	14.27	34.40	12.71	1.44
254		3.29	10.49	7.87	38.55	33.05	9.18	29.97	12.70	1.44
303		3.29	10.38	7.88	43.40	37.47	9.85	29.40	12.58	1.35
253		3.34	9.51	8.05	67.50	44.45	13.20	27.49	10.91	1.30
255		3.18	9.10	8.31	73.50	48.60	14.40	28.14	10.53	1.25
257		3.11	10.12	8.04	38.55	32.65	9.15	30.10	12.72	1.35
251		3.01	9.07	8.05	53.55	41.65	12.55	26.98	11.20	1.36
250		3.37	10.90	8.79	26.20	24.85	8.53	34.35	13.76	1.52
LUC	Mores Island	3.09	9.42	8.10	42.02	32.10	10.40	30.26	11.62	1.43

TABLE 1 [CONTINUED]

4th whorl height	4th–6th height	umbilical width	lip width	lip thickness	aperture height	aperture width	protrusion	tilt	weight	aperture-suture
6.65	10.92	4.63	1.22	1.09	8.83	7.25	2.50	1.64	.79	4.42
6.88	11.64	4.55	1.23	1.09	9.31	7.73	2.47	1.82	.73	5.13
6.84	11.52	4.52	1.22	.88	9.05	7.42	2.10	1.82	.68	4.83
6.15	9.71	4.30	.98	.65	8.81	7.15	2.62	2.15	.49	4.51
6.08	9.87	4.64	.91	.63	9.38	8.01	2.43	1.98	.71	5.51
6.25	10.01	4.38	1.13	.73	9.12	7.41	2.54	2.05	.62	5.01
6.26	10.17	5.48	1.21	1.14	11.10	8.99	3.15	1.95	1.49	6.30
6.03	10.28	4.93	1.11	.84	10.19	8.50	2.81	2.06	.96	5.73
6.10	8.79	4.94	.95	.62	9.76	8.10	2.31	1.87	.82	5.42
5.38	7.49	4.12	.85	.44	7.86	6.63	2.13	2.21	.37	3.79
6.22	10.59	5.19	.98	.69	10.73	9.07	2.78	2.04	1.12	6.18
6.57	11.06	5.14	.99	.75	10.65	8.96	2.64	2.11	1.36	6.23
6.60	10.03	3.13	.71	.52	7.51	6.49	1.93	2.15	.41	5.05
6.68	9.53	4.49	.96	.63	9.49	7.68	2.76	2.30	.81	5.49
6.24	9.42	4.74	.99	.74	9.72	7.87	2.75	2.20	.83	5.39
6.59	11.10	5.59	1.38	1.47	11.94	9.29	3.35	2.19	1.48	6.01
6.42	10.70	5.19	1.14	.91	10.77	8.61	3.06	2.40	1.21	5.41
6.65	10.49	4.68	1.06	.85	10.18	8.21	2.86	2.28	.89	4.91
6.74	11.57	4.96	1.18	1.20	11.42	9.18	3.23	2.40	1.11	5.85
6.50	10.73	5.91	1.46	1.32	12.61	10.13	4.01	2.81	1.34	5.96
6.44	10.63	4.23	1.13	1.04	9.41	7.94	2.64	2.00	.84	5.24
6.72	10.44	4.49	1.06	.84	9.38	8.11	2.93	2.65	.62	4.82
6.69	10.63	4.81	.99	.83	9.51	8.24	2.69	2.19	.69	5.12
6.35	9.88	4.73	.90	.74	9.44	7.76	2.62	1.99	.69	5.14
6.64	10.08	6.03	.96	.83	11.16	9.08	2.74	1.86	.98	5.69
6.66	9.43	5.25	1.47	.92	11.50	9.34	2.78	2.26	1.12	5.63
6.34	10.11	5.95	1.13	1.21	11.18	9.05	3.88	2.49	1.15	5.26
6.58	10.96	3.83	1.02	1.06	9.93	8.37	2.67	2.19	1.00	5.99
7.38	10.45	4.43	.98	1.38	9.95	8.08	3.29	2.39	1.12	5.89
6.48	10.06	4.93	.96	1.11	9.93	8.31	3.14	2.31	1.13	5.28
6.83	11.58	5.13	1.06	1.17	10.58	9.11	3.15	2.15	1.15	5.88
6.89	11.18	4.43	.85	.87	9.78	8.24	2.95	2.40	.87	5.35
6.81	11.30	5.63	1.12	1.09	11.25	9.08	3.06	2.09	1.39	5.85
6.73	11.63	5.63	1.09	.84	10.73	8.71	3.00	2.03	1.06	5.44
6.77	12.08	5.16	.95	.79	10.23	8.40	2.71	2.05	.95	5.82
6.74	12.04	5.31	1.17	.89	10.59	8.97	2.82	1.95	1.13	6.20
6.84	12.42	5.98	1.20	1.07	11.28	9.23	2.98	1.85	1.58	6.27
6.47	11.73	5.56	1.14	.67	10.53	8.84	2.89	2.27	.76	5.41
6.26	10.40	5.34	1.01	.72	10.50	8.74	2.67	2.20	.86	5.58
7.04	13.28	6.18	1.15	1.04	11.76	9.31	3.18	1.83	1.71	6.15
6.76	12.16	5.81	1.32	1.25	11.95	9.72	3.22	2.37	1.70	6.53
6.62	11.73	5.60	1.21	1.01	11.21	8.95	3.11	2.20	1.08	5.84
6.84	12.73	6.71	1.54	1.61	12.91	10.29	3.51	2.41	2.13	6.24
6.27	10.30	6.19	1.15	.88	12.39	10.19	3.41	2.21	1.36	6.73
7.54	13.26	5.95	1.40	1.38	12.23	10.29	3.36	2.50	1.83	6.15
7.15	13.35	6.33	1.53	1.55	12.37	10.23	3.40	2.12	1.48	6.29
6.98	11.49	5.37	.99	1.08	10.89	9.07	3.07	2.21	1.01	5.48
6.80	10.98	5.18	.98	.98	10.72	8.75	3.15	1.99	.98	5.59
7.20	12.87	6.23	1.61	1.15	12.53	10.43	3.24	2.14	1.80	5.89
6.80	11.41	4.79	1.15	1.43	10.66	8.93	2.95	2.31	1.34	5.82
7.20	12.11	6.62	1.93	1.84	13.14	11.23	3.73	2.12	2.07	6.41
7.36	12.48	5.89	1.55	1.60	11.71	9.77	3.49	2.19	1.54	5.99

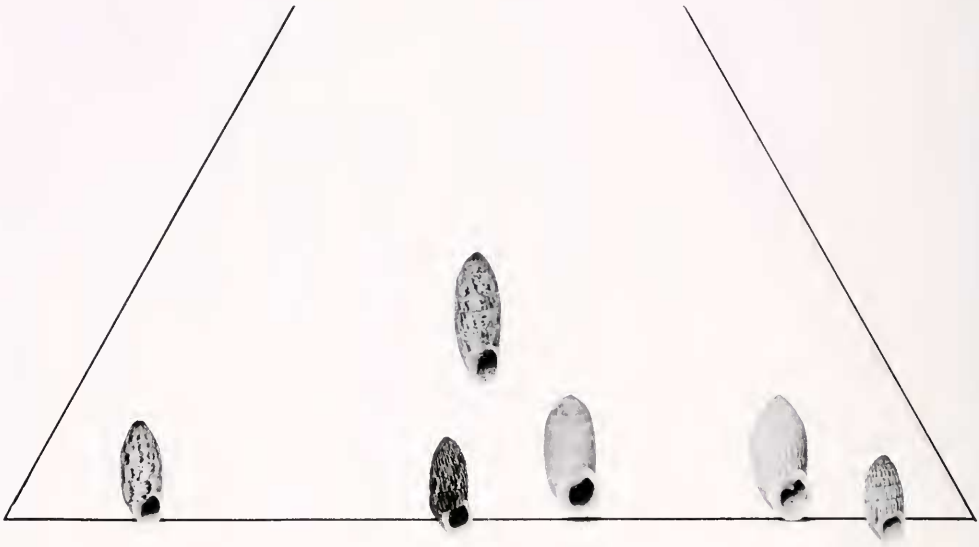

Figure 7. Representative shells for samples depicted in same positions on Fig. 6. At bottom line, left to right: locality 230 (typical *C. bendalli*); locality 316 (convergent *C. bendalli* from Pongo Carpet); locality 253 (intermediate shell from The Crossing); locality 254 (*C. abacoense*); "*C. chrysaloides*" from Grand Bahama. Above: locality 204 (*C. bendalli* from Grand Bahama).

tion) are *C. bendalli* from Grand Bahama. The third axis divides samples of *C. bendalli* (the mottled morphotype) into its two isolated areas.

The matrix of factor scores (Table 2) permits us to infer the basis of separations in Figure 6 (consult the matrix of mean values—Table 1—for the raw information). Only three variables score highly on the first axis. (This axis serves as a dimension of reference for the mottled morphotype, *C. bendalli*. Samples of *C. bendalli* load strongly upon it, and weakly upon the second axis—see Figs. 6–7.) Not surprisingly, these three variables are the ribbing measures 4–6. (Mottled samples always have much weaker ribs than ribby samples, but the ribs are always far more numerous in mottled samples; all our ribbing measures are counts.) No other variable so consistently separates *C. bendalli* from *C. abacoense*. The second axis, with it high loadings for *C. abacoense* (the ribby morphotype), contains high scores for most measures of final size and whorl size. (The scores are negative in this case. The sign is of no particular importance, since it only indicates the direction of the reference vector. The pattern of scores and loadings would not change if the vector pointed 180° in the opposite direction, thus reversing all the signs.) To some extent, this suite of high scores only mirrors the distinction by ribbing made on the first axis. Since reference vectors are normalized, a small number of ribs must lead to a greater contribution to the vector from other measures. But the ordering of intensity within this group of high scores clearly distinguishes the primary characteristics of *C. abacoense*. Shells of *C. abacoense* do not have more whorls than *C. bendalli* (note small positive score for whorl number—primarily due to low whorl numbers of small "*C. chrysaloides*"), and they are not generally taller (modest score for shell height). The highest scores belong to measures of size that best distinguish the two taxa by higher mean values

Table 2. Factor scores of original variables upon the three factor axes used to depict samples in figure 6.

1. protoconch width	0.155	−0.102	−0.206
2. 4th whorl width	0.070	−0.228	−0.191
3. total whorls	0.280	−0.007	−0.387
4. 4th ribs	0.536	0.162	0.122
5. 6th ribs	0.491	0.149	0.030
6. 1st ribs	0.492	0.108	0.153
7. height	0.129	−0.187	−0.292
8. width	0.053	−0.247	−0.182
9. protoconch height	0.078	−0.204	0.283
10. 4th-height	0.072	−0.341	0.514
11. 4th–6th height	0.025	−0.362	0.344
12. umbilical width	0.071	−0.273	−0.149
13. lip width	−0.018	−0.236	0.041
14. lip thickness	−0.025	−0.272	0.122
15. aperture height	0.062	−0.258	−0.182
16. aperture width	0.047	−0.226	−0.175
17. protrusion	0.087	−0.200	−0.106
18. tilt	0.239	−0.040	0.102
19. weight	−0.003	−0.242	−0.158
20. aperture-suture	0.119	−0.265	−0.036

for *C. abacoense.* Shells of *C. abacoense* are heavier (measure 19), and wider both in spire (8) and umbilicus (12); they have a larger aperture (15–16) with a more strongly developed lip (13–14); finally, they are taller at standardized whorl numbers during middle portions of ontogeny (10–11). Thus, most of the information in this large matrix reduces to a single contrast between mottled (*C. bendalli*) and ribby (*C. abacoense*) morphotypes.

The third axis contains only 8.2 per cent of the total information, but it also displays a significant separation *within* the mottled morphotype, *C. bendalli.* With a single exception (sample 249, a peculiar, very large and many-whorled, interior sample of Abaconian *C. bendalli*), all samples with strong loadings are from Grand Bahama. Factor scores for this axis display a pattern of covariation found throughout the genus (Gould *et al.*, 1974; Gould and Paull, in press): whorl number (3) and shell height (7) are in negative association with measures of size at standardized whorl numbers. Shells become large either by growing large whorls (2, 10–11) or many whorls (3 and 7). Shell height reflects whorl number because shells add height but not width during later growth; maximum width is reached early in ontogeny in this genus named for a beehive. If final size can vary only within narrow limits, then these two alternate pathways to a given size must covary negatively. The primary geographic differentiation within *C. bendalli* on Little Bahama Bank has apparently followed this common pattern of covariance. Populations on Grand Bahama have taken the route of small whorls leading to high shells and many whorls (high scores for whorl number and shell height are matched by high loadings of the same sign for Grand Bahamian samples—Table 2 and Figs. 6–7). Abaconian samples reach the same sizes with fewer, larger whorls.

C) *Coherence of Regional and Local Patterns of Variation Within Morphotypes*

Our consistent discovery of coherent, broadly regional patterns of variation provides the primary datum for our rejection of the traditional view about *Cerion*—that its geographic variation is a "crazy-quilt" formed by haphazard shifting about of hundreds of species via hurricanes. We have never failed to detect a hierarchy of geographic coherence:

i) broad contiguous regions including several islands have distinctive morphologies. *C. striatellum*, the only *Cerion* throughout the eastern regions of its range (Hispaniola to the Virgin Islands), exhibits a clinal pattern of variation with increasing departure from "normal" morphology away from major centers of distribution in Cuba and the Bahamas (Gould and Paull, 1977). *Cerion uva*, the only species on the outlying islands of Aruba, Bonaire, and Curaçao, is sufficiently distinct to warrant its own subgenus in the traditional classification (Pilsbry, 1902).

ii) islands within broad regions are unambiguously, if subtly, distinct. The most important discriminator of eastern cerions, the first canonical axis of 23 samples, un-

covers the clinal pattern reported above (Gould and Paull, 1977), but subsequent axes clearly sort each island from all others with no overlap. *Cerions* of Aruba, Bonaire, and Curaçao also cluster by island (Baker, 1924; Gould, 1969).

iii) contiguous geographic subregions within islands can also be identified by very minor, but thoroughly consistent, patterns of character means and covariation; the more isolated the subregion, the more distinct the morphology. The narrow "waist" of Curaçao, for example, separates populations of *C. uva* into two distinct groups (Gould, 1969).

We will not venture any speculation about adaptive values, importance of founders, etc., but it does seem clear that geographic isolation is the primary correlate of morphological variation within taxa of *Cerion*. These patterns of geographic variation, by their stability and coherence, also indicate that episodes of transport and colonization have been rather less frequent than tradition dictates.

The geographic variation of Little Bahama Bank cerions conforms fully with these new expectations of coherence. We confine our comments to the mottled morphotype, *C. bendalli* since regional patterns have never been demonstrated within it before. We do not have enough samples of *C. abacoense*, and we have not seen two of its three major populations in the field—Mores Island and the apparently extinct population of Grand Bahama. Nonetheless, traditional taxonomy has already recognized the geographic coherence of four areas—Grand Bahama, Mores Island, southern tip of Abaco, and southeastern coast of Abaco. We reject the names, but confirm the distinction in our morphometric analysis.

1. Separation of *C. bendalli* from Grand Bahama and Abaco. Figure 6 demonstrates the morphological distinction of the two islands (see discussion above). We are particularly pleased to note that the basis of separation is not a few static adult features of unknown significance, but alternate pathways of a major pattern in covariance found throughout the genus.

Table 3. Factor scores of original variables upon the first Q-mode axis for *C. bendalli* from Grand Bahama.

1. protoconch width	0.249
2. 4th whorl width	0.289
3. total whorls	0.188
4. 4th ribs	–0.129
5. 6th ribs	–0.077
6. 1st ribs	–0.075
7. height	0.259
8. width	0.295
9. protoconch height	0.189
10. 4th height	0.178
11. 4th–6th height	0.245
12. umbilical width	0.255
13. lip width	0.212
14. lip thickness	0.181
15. aperture height	0.282
16. aperture width	0.311
17. protrusion	0.201
18. tilt	–0.051
19. weight	0.240
20. aperture-suture	0.301

2. The regional pattern on Grand Bahama. As we collected on Grand Bahama, it seemed to us that patterns of morphology followed general trends throughout the island. Shells of northern samples were small, particularly in coastal populations near mangrove areas. (This is another consistent pattern within the mottled morphotype. Mottled shells are also dwarfed on the low, bank-interior western coasts of Andros, Eleuthera and Great Exuma).

We used trend surface analysis to test a hypothesis of simple regional patterns. This technique widely employed by geologists but little known among biologists (Marcus and Vandermeer, 1966), performs a multiple regression analysis of a morphological feature (dependent variable) against independent variables expressed as geographic coordinates. Increasingly more complex surfaces are obtained by adding terms in a polynomial expansion of the X and Y coordinates. Predictions from the best fit surface are compared with actual values to generate a vector of residuals that defines

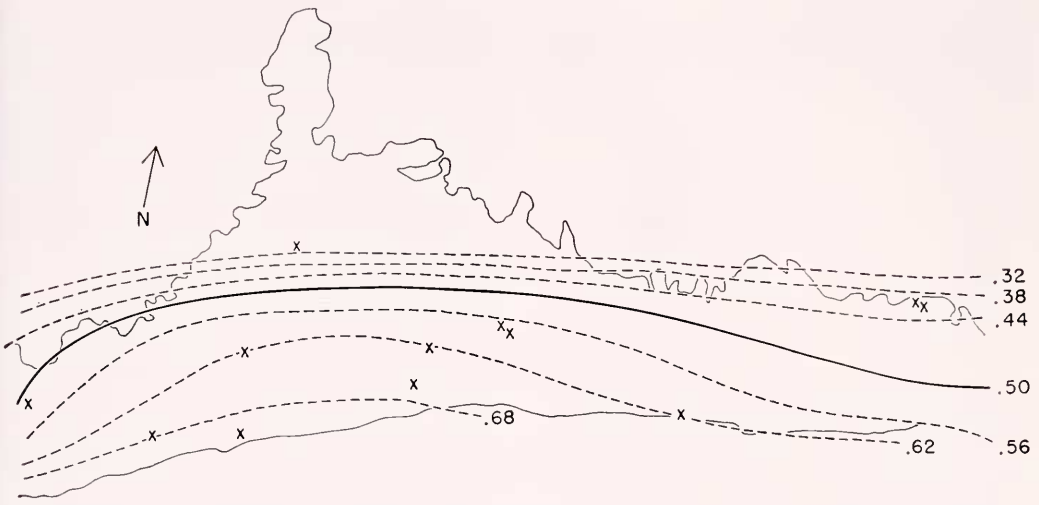

Figure 8. Third order trend surface analysis (with interaction terms suppressed) for projection of Grand Bahamian samples on the first varimax axis of a Q-mode analysis; this is a "size" axis based on all variables. Note simple pattern of increasing size from north to south, with more rapid transition near the northern coast, where dwarfed samples pass rapidly to interior samples of modest size. Actual localities indicated by crosses. This smooth variability has, in the past, been parcelled among three separate species defined only by differences in size.

"goodness of fit." The "art" of trend surface analysis involves the selection of a fit that explains enough information, yet remains sufficiently simple to represent a truly regional pattern. Points can be fit exactly with polynomial surfaces of sufficiently high order. We used the program of Lee (1969).

We decided not to use the mean of individual characters as dependent variables, but a value expressing major determinants of covariance among samples. Consequently, we performed a Q-mode factor analysis of all *C. bendalli* samples from Grand Bahama and used loadings on the first varimax axis (for a three-axis solution) as the dependent variable. This single axis encompasses 57.2 per cent of the variance among 20 characters for the 12 samples. Factor scores of variables upon it (Table 3) show that it represents a fairly "pure" size axis, with high and similar loadings for measures of final size and whorl size. (We do not detect the common negative interaction here, because we do not consider alternate pathways to a similar final size. We have, instead, the opposite situation—a wide range of mean shell size from very small on the north coast to quite large elsewhere. The dwarfed shells have both few whorls and small whorls.)

The first order fit alone has a multiple correlation of .82 for a coefficient of determination, $r^2 = .67$. A simple sloping plane encompasses ⅔ of all geographic variation expressed by the most important single dimension based on all 20 measured characters. As expected, the axis runs almost due E-W with smaller values to the north. Figure 8 represents our highest surface, a third order fit with interaction terms suppressed (X_1X_2, $X_1^2X_2$, and $X_1X_2^2$—we did not have enough sample points for the degrees of freedom needed to fit them). This surface yields a multiple correlation of .934, for a coefficient of determination, $r^2 = .87$. Even at this level of potential complexity, the surface represents a surprisingly smooth cline from small northern shells to larger southern shells. Contour lines follow the

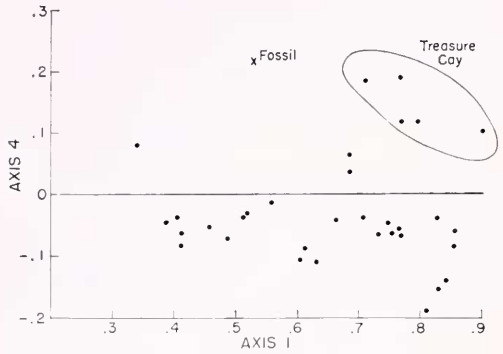

Figure 9. Factor loadings on the first and fourth axis for all samples of Little Bahama Bank cerions. Although the fourth axis explains less than 1 per cent of the total variance among samples, it separates both the Treasure Cay populations and the single fossil sample from all others.

island itself, while bunching of lines at the northern coast indicates the rapid transition from coastal dwarfs to interior shells of modest size that we observed in the field. (Though we had noticed the coastal phenomenon, we did not expect the regional pattern to be so simple.) We detected no geographic pattern in the vector of residuals.

3. Distinction of subareas on Abaco. With more than 30 samples of *C. bendalli* from Abaco, we could detect more local patterns of distinction, also correlated with geographic isolation.

i) small, ribby shells of Pongo Carpet. We have already reported in detail on a semi-isolated coastal area well within the range of *C. bendalli* (Gould, Woodruff, and Martin, 1974). Here, along nearly 7 km of eastern coast, we find a small, heavy, fairly ribby morphology partly convergent on *C. abacoense*. (We included only one Pongo Carpet sample in this study; it has the highest loading of any pure *C. bendalli* sample upon the *C. abacoense* axis—Fig. 6.) This Pongo Carpet morphology is most distinct in its southern area of greatest isolation, and varies in a clinal fashion towards "normal" morphology as it approaches the northern zone of contact. It cannot be distinguished genetically from surrounding populations of standard morphology. In fact, it shares *with* these surrounding normal populations the only distinctive genetic marker (the rare Mdh-2^a allele) of its area—Mdh-2^b is fixed in all other populations of *C. bendalli*. Although these Pongo Carpet shells clearly merit specific distinction on all previous criteria, we cannot regard them as any more than a local variant within a coherent taxon.

ii) populations on Treasure Cay. The difference between statistical and biological significance is rarely appreciated. Morphometricians routinely ignore axes of variation that encompass too little variation to win statistically significant distinction from zero. Yet minor patterns can be very real in a biological sense. Suppose that we have a large matrix with many samples and variables, and that a few samples from a geographically isolated region gain distinction from all others by consistent differences in just a few covarying characters. Suppose also that this distinction is not evident in qualitative observation. The information recorded by this distinction may include far less than 1 per cent of the total matrix; yet it is highly significant from a biological point of view, especially since it is so easily missed in raw data or qualitative observation. The criterion for importance must be correlation with geography, not per cent of information.

We offer such a case in the semi-isolated samples of Treasure Cay (Fig. 3). The fourth axis of our Q-mode analysis for all samples encompasses only 0.95 per cent of all information. Yet a plot of loadings upon the fourth axis clearly separates all Treasure Cay samples from all others with no overlap (Fig. 9). Loadings for the Treasure Cay samples never exceed 0.2, so the distinction arises from less than 4 per cent of the information (squared loading) in these populations. Factor scores for this axis (Table 4) indicate that the separation of these samples arises from their high values for protoconch height and, to a lesser extent, whorl number.

iii) temporal variation. The carbonates of Little Bahama Bank islands are largely marine, and we do not find the soil zones with abundant fossil cerions so common on other islands. But we did collect one fossil sample from an aeolianite in a cut on the road leading to Snake Cay. We are especially pleased to report that this sample can be distinguished clearly from all modern populations, though its general appearance links it unambiguously with living forms of its area. As a strongly and fairly sparsely ribbed sample of general *C. bendalli* shape, its mean morphology gives it an intermediate position in the essential distinction of the two morphotypes (Fig. 6). Its uniqueness is apparent in Fig. 8. It shares, with Treasure Cay samples, the joint high values of protoconch height and whorl number (in fact, its loading on the fourth axis is maximal among all samples), but it differs from them in its weaker loading on the first axis (i.e., its greater affinity with the ribby morphotype).

The study of fossil cerions is yielding important information on the stability of modern patterns of geographic variation within taxa. In all three cases studied so far, fossil samples share the same basic morphology of modern populations, but the fossils occupy presently unrealized portions of the morphological spectrum (*C. rude* of St. Croix vs. all living eastern cerions, Gould and Paull, 1977; *C. uva* from Indian shell middens on Curaçao, Gould, 1971; and this Snake Cay Road sample).

A note on technique: A potentially valid objection has been raised against much work in multivariate morphometrics: available techniques for separation are now so numerous and varied that proper selection may be able to affirm nearly any a priori preference. Robust conclusions may require the joint confirmation of several techniques. Readers may criticize our distinctions by pointing to unusual features of our factor analytic model; we use a Q-technique in I-space while most workers prefer more conventional R-mode analysis in A-space

Table 4. Factor scores for the 4th Q-mode axis to illustrate the basis of distinction (in covariance) for the Treasure Cay samples.

1. protoconch width	−0.131
2. 4th whorl width	−0.243
3. total whorls	0.477
4. 4th ribs	−0.097
5. 6th ribs	−0.012
6. 1st ribs	−0.131
7. height	0.118
8. width	0.015
9. protoconch height	0.735
10. 4th height	0.036
11. 4th–6th height	−0.212
12. umbilical width	0.044
13. lip width	0.089
14. lip thickness	−0.011
15. aperture height	−0.084
16. aperture width	−0.068
17. protrusion	−0.159
18. tilt	−0.090
19. weight	−0.114
20. aperture-suture	−0.026

(Sneath and Sokal, 1973, p. 116). We normalize vectors to eliminate size explicitly, while most studies include these differences. Finally, we equalize weights of variables with an uncommon transformation, while most studies use raw data or transform with different techniques. Consequently, we redid the analysis in the R-mode with no normalization or character weighting (using BMD program P4M).

The factor loadings (Table 5) display the same pattern as the factor scores of our Q-mode analysis with two interesting exceptions, one expected. The first axis of the R-mode analysis reflects shell size, the variation explicitly eliminated in our Q-mode analysis. The fourth axis displays a pattern of covariance often seen in *Cerion* (Gould *et al.*, 1974), but not encountered in our Q-mode analysis. We find joint high loadings for four variables: apertural protrusion and tilt (17–18) and lip width and thickness (13–14). When we specified our measures before beginning this study, we selected these as potentially correlated traits expressing the intensity of changes in

Table 5. Factor loadings of original variables for an R-mode analysis of all Little Bahama Bank samples.

	1	2	3	4	5
1. protoconch width	0.789	0.441	0.016	–0.021	0.190
2. 4th whorl width	0.931	–0.037	0.226	0.013	0.018
3. total whorls	0.329	0.288	–0.864	0.074	0.108
4. 4th ribs	–0.150	0.943	–0.195	0.083	–0.071
5. 6th ribs	–0.085	0.927	–0.268	–0.006	–0.048
6. 1st ribs	–0.144	0.918	–0.172	0.087	–0.078
7. height	0.900	0.000	–0.332	0.189	0.136
8. width	0.941	–0.251	0.015	0.033	0.099
9. protoconch height	0.200	–0.120	0.017	0.043	0.955
10. 4th height	0.305	–0.302	0.698	0.272	0.388
11. 4th–6th height	0.541	–0.412	0.709	0.102	–0.018
12. umbilical width	0.876	–0.269	–0.051	0.150	0.038
13. lip width	0.565	–0.536	0.001	0.407	0.164
14. lip thickness	0.485	–0.437	0.202	0.593	0.166
15. aperture height	0.909	–0.167	0.021	0.328	0.076
16. aperture width	0.910	–0.162	0.062	0.300	0.138
17. protrusion	0.689	–0.071	0.020	0.648	–0.018
18. tilt	0.090	0.407	0.019	0.809	0.017
19. weight	0.822	–0.318	0.113	0.299	0.072
20. aperture-suture	0.849	–0.070	0.135	0.023	0.147

growth that mark secretion of the adult aperture (intense change in coiling direction should be associated with a stronger lip). We are gratified to see their joint association on an axis mathematically independent of shell size. It would be less enlightening to find that intense development correlated only with large shell size. The association of size and adult development exists to be sure (13, 14, and 17 also load highly on the size axis), but the fourth axis displays the partial independence of adult development.

The other axes are essentially identical with the factor scores of our Q-mode analysis. Axis 2 reflects the differences in ribbing that produced the basic separation of mottled and smooth morphotypes in our Q-mode analysis (axis 1); axis 3 records the negative association of whorl number and shell height with measures of whorl size that separated Grand Bahamian and Abaconian *C. bendalli* in our Q-mode analysis (axis 3); finally, axis 5 makes the same separation of the Treasure Cay and Snake Cay Road fossil samples from all others, primarily on the basis of protoconch height.

When we consider factor scores to see how these R-mode axes sort samples, we find virtual identity with our loadings of Q-mode analysis. The first axis is different, since we eliminate its effects by normalization of sample vectors in our Q-mode analysis. The R-mode first axis merely sorts samples by shell size—a biologically unenlightening distinction in this case. But axes 2, 3, and 5 make the same separations as corresponding axes in the Q-mode analysis. The correlation coefficients (at $N = 52$) for R-mode scores with Q-mode loadings for corresponding axes are .87 for R-mode 2 with Q-mode 1 (ribbing) to separate the morphotypes; .60 for R-mode 3 with Q-mode 3 (negative interaction of whorl number and whorl size to separate Grand Bahama and Abaco *C. bendalli*); .72 for R-mode 5 with Q-mode 4 (to separate Treasure Cay and Snake Cay Road fossil samples from all others). We are therefore confident that our Q-mode patterns identify real and important distinctions in nature, robust with respect to techniques used to identify them, and not artifacts of unusual multivariate procedures.

Table 6. Univariate ANOVA for discriminatory power of original variables in samples of the hybrid zone at Rocky Point. Univariate F-ratios with 4 and 89 degrees of freedom.

Variable	among mean sq.	within mean sq.	F-ratio	Probability
1. protoconch width	23.33	9.59	2.43	0.5242E–01
2. 4th whorl width	136.52	20.35	6.71	0.2163E–03
3. total whorls	0.25	0.14	1.83	0.1299E+00
4. 4th ribs	1046.82	32.45	32.26	0.1014E–07
5. 6th ribs	608.14	18.56	32.77	0.9304E–08
6. 1st ribs	18.53	2.76	6.72	0.2131E–03
7. height	36.94	2.80	13.22	0.2309E–05
8. width	5.87	0.32	18.27	0.2895E–06
9. protoconch height	5.64	6.46	0.87	0.5149E+00
10. 4th height	16.83	13.50	1.25	0.2963E+00
11. 4th–6th height	3.84	0.99	3.89	0.6083E–02
12. umbilical width	265.17	29.25	9.07	0.2865E–04
13. lip width	59.04	18.88	3.13	0.1843E–01
14. lip thickness	85.70	19.15	4.47	0.2774E–02
15. aperture height	465.77	28.87	16.13	0.6345E–06
16. aperture width	166.91	20.18	8.27	0.5324E–04
17. protrusion	32.23	10.79	2.99	0.2271E–01
18. tilt	14.48	8.33	1.74	0.1474E+00
19. weight	2.04	0.05	40.03	0.3185E–08
20. aperture-suture	169.07	27.66	6.11	0.3978E–03

D) *Interaction Between Morphotypes*

We recorded the areas of interaction between ribby (*C. abacoense*) and mottled (*C. bendalli*) morphotypes in our discussion of geographic distribution (pp. 376–377). We identified these areas before performing any multivariate analysis upon the shells. Thus, the intermediate position of all these samples in the contrast between ribby and mottled morphotypes (axes 1 and 2 of our Q-mode analysis) serves as a strong confirmation of interaction. The intermediate field of Figure 6 is shared by only two other samples: the convergent Pongo Carpet sample (No. 316) lies on the border of mottled and intermediate samples; secondly, the fossil sample (No. 246) occupies an intermediate position.

All other points in the intermediate zone belong to samples in areas of geographic contact between the morphotypes. These include:

1. the sample from Sandy Point Village (Fig. 6) marking the transition from exterior to interior coast (sample 251).

2. samples from the main road at The Crossing (Fig. 6—samples 253 and 255) where interior *C. bendalli* is separated by 500 m and a narrow hill from coastal *C. abacoense*. We did not record these in the field as intermediate in morphology; they appeared to us at the time as somewhat peculiar *C. bendalli*. Their intermediate position on Figure 6 indicates that some leakage occurs in this area of closest geographic contact between morphologies apparently separate in the field.

3. the hybrid zone at Rocky Point. We noted in the field that the transition from southern ribby to northern mottled seems to occur in the narrow area between samples 305–260. We are therefore pleased to demonstrate a smooth transition in morphology, spanning the entire range from pure ribby to pure mottled, along the geographic sequence in this area: 305-306-307-308-260 (Fig. 6). Our impression that the effects of hybridization do not spread far south of 305 seems to be affirmed by the non-clinal positions of the next two southern samples, 304 and 259. Finally, the interior samples of *C. bendalli* collected in the area of coastal hy-

Table 7. Matrix of Mahalanobis D^2 distances for samples of the hybrid zone at Rocky Point.

	305	306	307	308	260
305	0.0				
306	8.81493	0.0			
307	19.71928	6.93176	0.0		
308	27.42574	14.81611	5.17647	0.0	
260	36.26627	19.43301	10.82527	4.94755	0.0

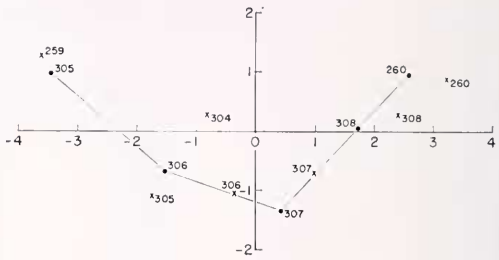

Figure 10. Samples from the hybrid zone at Rocky Point projected on the first two axes of a discriminant analysis. Points represent an analysis based only on samples that, from our field impressions, constitute the zone of transition (numbers 305-306-307-308-260 from south to north). Note the smooth transition along the first axis (74.3 per cent of all information). Crosses represent a separate analysis (shown here on the same scales) for these samples plus two more southern samples in the same area (304 and 259). Sample 304 breaks the morphological cline, thus confirming our impression that it is beyond the localized zone of interaction.

bridization confirm the localization of interaction. Sample 310, collected 400 m from the coast between sample 305 (the pure ribby beginning of the hybrid zone) and sample 306 lies among mottled samples, but near the periphery of mottled and intermediate forms. Sample 309, about 600 m inland from 310, is well within the *C. bendalli* cluster and shows no signs of intermediacy.

We then performed a discriminant analysis on samples of the hybrid zone, using D/DA, a program written by John Rhoads, Dept. of Anthropology, Yale University (see Gould et al., 1974 for more details). In the field, we had concluded that the morphological effects of hybridization are confined to a small, coastal area at Rocky Point (Fig. 5). We therefore performed our analysis on the five samples collected along this mile of coast (from south to north, 305, 306, 307, 308, and 260).

The table of univariate ANOVA's (Table 6) shows that the best discriminators are measures of ribbing and shell size—scarcely surprising since shells of *C. bendalli* are characteristically smaller and more copiously (though more weakly) ribbed than those of *C. abacoense*.

As a first indication of evenly clinal patterns, the matrix of Mahalanobis D^2 distances (an overall measure of similarity based on all characters with variance and covariance adjustments) exhibits a smooth morphological transition along the geographic axis of collections (Table 7). Figure 10 represents a plot of all samples against the first two discriminant axes. The first axis, which encompasses fully ¾ (74.3 per cent) of all information, arrays the samples in a smooth and gradual transition. The second axis (only 13.2 per cent) produces the "horseshoe pattern" so commonly seen when two axes exhaust nearly all information (Reyment, 1975). (If end-member samples have high values on the main discriminator and intermediate samples lie close to zero, then the second axis must emphasize these intermediate samples.)

The table of discriminant loadings displays the patterns of covariance that separate samples (Table 8—these loadings are correlations of original variables with new axes, not coefficients of the discriminant axes themselves). Ribbing (positive loadings) and adult size (negative loadings) dominate the first axis. Northern (*C. bendalli*) samples with their numerous ribs and small shells have high positive projections upon this axis. Moving southward through the hybrid zone, shells gradually become larger as ribs become sparser and stronger. (Measures of ribbing and size are invariably independent as patterns of covariance within samples—see Gould et al., 1974. They are united as joint discriminators of the morphotypes in this study of among sample covariance.) Loadings on the mi-

Table 8. Discriminant loadings of original variables upon axes used to separate samples of the hybrid zone at Rocky Point.

	1	2
1. protoconch width	−0.0377	0.1390
2. 4th whorl width	−0.2121	0.0888
3. total whorls	−0.0300	−0.1247
4. 4th ribs	0.5185	0.3257
5. 6th ribs	0.5322	0.2315
6. 1st ribs	0.2313	0.1053
7. height	−0.3043	0.0137
8. width	−0.3785	−0.0351
9. protoconch height	−0.0767	−0.0508
10. 4th height	−0.0965	0.0967
11. 4th–6th height	−0.1753	0.0695
12. umbilical width	−0.2312	0.2911
13. lip width	−0.1008	−0.1465
14. lip thickness	−0.1716	−0.0549
15. aperture height	−0.3355	0.2920
16. aperture width	−0.2413	−0.0571
17. protrusion	−0.1074	0.2179
18. tilt	0.1210	0.0371
19. weight	−0.5706	0.1420
20. aperture-suture	−0.1840	−0.3474

nor, second axis make little biological sense to us; they seem to represent a concatenation of those variables that distinguish, in a minor way, the intermediate samples from both endpoints. Thus, any measure that distinguishes *either* endpoint has a relatively high loading (ribs and size now have joint positive loadings), while three disparate measures with generally higher values in the intermediate samples (variables 3, 13, and 20) have negative loadings.

As a final example of smooth transition, Table 9 presents a matrix of classification. Seventy-nine of 94 specimens lie nearest to their own sample centroids (84 per cent). Every misclassified individual groups with a geographically adjacent sample.

This smooth transition is matched by a total lack of evidence for any increased variability in intermediate samples (as we might expect in a "classic" hybrid zone—Mayr, 1963). Table 10 presents C.V.'s for all 5 samples and for typical samples of "pure" mottled and ribby shells in the central areas of their distribution.

In an attempt to learn whether the smooth morphological transition continues southward beyond our perception of it in the field, we performed a similar analysis on 7 samples—the 5 used before plus 304 and 259, the next southern coastal samples (Fig. 10). The first axis is virtually unchanged in both loadings and discriminatory power. As the previous factor analysis indicated (Fig. 6), the next southern sample (304) breaks the smooth transition by plotting closer to the *C. bendalli* axis than sample 305 directly to the north.

Table 9. Classification (hits and misses) table for discriminant analysis of samples from the hybrid zone at Rocky Point. Total hits = 79 out of 94 possible. Rate = .8404.

	305	306	307	308	260
305	18.	0.	0.	0.	0.
306	2.	15.	2.	0.	0.
307	0.	1.	17.	1.	0.
308	0.	0.	3.	11.	4.
260	0.	0.	0.	2.	18.

This morphometric analysis cannot resolve the key question of appropriate biological status for populations of the two morphotypes. Are they imperfectly separated entities meriting taxonomic recognition as semispecies or simple geographic variants with uneventful and unrestricted mixture at points of contact? The habitat preferences and coherence in areas of near contact (The Crossing) might argue for separation, and the very localized nature of the hybrid zone would support such an assertion. But rapid transitions and step clines occur within coherent taxa (Endler, 1977). We must turn to genetic analysis for further enlightenment.

IV. ALLOZYME VARIATION OF *CERION* ON THE LITTLE BAHAMA BANK

A. Introduction

The practice of combining electrophoresis with histochemical staining methods to study variation of enzymes is now well established. The applicability of this meth-

Table 10. Coefficients of variation for hybrid zone samples and for representative samples of *C. bendalli* and *C. abacoense* from the center of their ranges

	central *bendalli*	b		hybrid zone		a	central *abacoense*
	214	260	308	307	306	305	250
1. protoconch width	6.3	4.7	5.7	5.9	6.2	4.8	5.2
2. width of 4th whorl	5.4	5.2	4.6	7.3	7.1	4.8	6.1
3. total whorls	4.9	4.7	5.1	5.0	5.2	4.7	5.6
4. ribs fourth whorl	19.5	10.8	12.9	11.2	11.6	12.0	11.0
5. ribs sixth whorl	20.1	10.4	11.9	10.4	8.6	6.7	11.3
6. first ribs	22.3	12.0	11.8	13.8	16.6	18.4	19.4
7. shell length	8.0	6.2	6.9	4.5	6.3	6.8	6.8
8. shell width	4.1	3.6	4.9	5.0	5.8	4.4	4.3
9. protoconch height	14.0	9.4	9.5	10.5	12.3	10.5	8.8
10. height 4th whorl	5.4	5.2	6.3	9.0	6.9	6.3	8.0
11. height 4–6	7.6	9.3	9.4	9.8	11.3	10.3	8.3
12. umbilical width	8.0	12.3	12.3	13.1	11.6	12.0	9.9
13. lip width	15.3	14.9	27.0	19.3	22.2	23.0	14.4
14. lip thickness	31.1	32.5	18.8	24.7	26.0	26.6	24.1
15. aperture height	7.4	7.2	5.0	5.7	7.1	5.3	3.9
16. aperture width	6.5	5.8	4.9	6.9	6.9	6.4	5.5
17. protrusion	16.7	14.2	12.9	16.5	13.0	12.7	12.3
18. tilt	16.4	16.5	20.0	10.7	13.3	12.9	17.9
19. weight	27.0	25.8	14.2	15.3	14.1	15.3	13.9
20. aperture to suture	9.2	8.5	17.5	7.9	12.7	9.0	11.6

odology to current problems of evolutionary biology is well reviewed by Avise (1974), Lewontin (1974), and various authors in the volume edited by Ayala (1976). We originally applied this approach to *Cerion* in the hope that genic variability might be more conservative than shell form in these morphologically variable animals. In the following account, we will report our findings as they apply to the systematic problem of the relationship between ribby and mottled morphotypes. For convenience, these contrasting shell types will be referred to *C. abacoense* and *C. bendalli* respectively as suggested above. In subsequent papers, we will describe the genetic aspects of the interaction between these taxa in more detail (Woodruff and Gould, in press), and the relation between genic and phenic variation at the level of the individual, population, and species (Woodruff, in prep.).

Variation in the electrophoretic pattern of structural gene products was surveyed in 1,575 individual adult snails from 47 populations from the islands of the Little Bahama Bank. Localities are indicated in Figure 3. In most cases, these are the same localities described in the morphometric analyses presented above. Furthermore, whenever possible, we have examined the same individual snails. Sample preparation, biochemical specifics, and other technical aspects of the starch gel electrophoresis apparatus employed are described elsewhere (Woodruff, 1975b). In the context of this survey, we have examined 16 enzyme systems and some general proteins and interpreted the observed banding patterns in terms of at least 28 loci. Here we will describe the variation in 20 of these structural gene products: ones that we found to give reproducible and genetically interpretable patterns. Variation of these enzymes among the Little Bahama Bank *Cerion* is outlined in Table 11. While 14 of these proteins are monomorphic and are fixed for the same allele in both taxa, polymorphisms were detected in the remaining six. (Est-3 and Pgi are also variable allozymes but are excluded from this

discussion.) Variation in each case is due to a simple Mendelian system involving codominant alleles. In the absence of formal genetic crosses, our genetic interpretations are based on two criteria. First, phenotypic ratios (and presumed genotypic ratios) agree closely with Hardy-Weinberg expectations. Second, patterns of banding of particular enzymes correspond to simple models of molecular structure. In most cases, the inferred structures are similar to those of functionally analogous enzymes in other animals whose structures have been established by other techniques. The six polymorphic loci segregate independently of one another; this is quite reasonable as one species of *Cerion* is known to have 27 pairs of chromosomes (Burch and Kim, 1962).

Before proceeding with the results of this genetic survey, we wish to outline the general nature of population structure in *Cerion*. Beginning in 1973, Woodruff has been studying two large marked populations of *C. bendalli* and *C. abacoense* on Abaco (3 years' experience with over 1,500 individually marked snails). Generation time for *Cerion* is not well defined. Juveniles grow slowly and erratically and probably do not lay down the shell's adult lip until they are 3 years old. The duration of the adult phase is also poorly defined; multiple-recapture studies suggest that some adults live at least another 10 years. Snail distribution at the coastal study sites is patchy but averages 8–13 adults per square meter. Dispersal data are now being used to estimate various evolutionarily important parameters. Effective neighborhood size or effective population size (N of Wright, 1946) is about 1,000 snails. Neighborhood area is 50–100 m^2. Our preliminary estimate for gene flow (l of May et al., 1975) suggests that this variable will be shown to have a value of about 3 meters. This estimate is, however, based on the formula $l = x\sqrt{g}$ where x is the mean distance travelled in a generation and g is the probability of leaving a deme or neighborhood. While these parameters can be estimated fairly accurately in *Cerion*, the ultimate determinant of effective gene flow, reproductive success outside the deme of birth, will be very difficult to assess.

Table 11. Electrophoretically demonstrable allozymic variation in *Cerion* from the Little Bahama Bank.

Enzyme	No. of alleles
Variable Enzymes:	
Esterase-2 (Est-2)	7
Esterase-3 (Est-3)	*
Malate dehydrogenase-1 (Mdh-1)	2
Malate dehydrogenase-2 (Mdh-2)	2
6-Phosphogluconate dehydrogenase-1 (6-Pgdh)	2
Phosphoglucose isomerase (Pgi)	*
Glutamic oxalacetic transaminase (Got-1)	3
Leucine aminopeptidase (Lap)	3
Invariable enzymes: alcohol dehydrogenase (Adh), Est-1, Est-6, Est-7, isocitrate dehydrogenase-1 (Idh-1), Idh-2, α-glycerophosphate dehydrogenase (α-Gpdh), indophenol oxidase (Ipo), phosphoglucomutase (Pgm-1), Pgm-2, Got-2, acid phosphatase-1 (Acp-1), Acp-2, alkaline phosphatase-1 (Ap-1)	

* At least two alleles segregating; variation not yet interpretable.

One of the first things we were able to establish was that *Cerion*, a facultative hermaphrodite (Richter, 1926; Jaenicke, 1933), is apparently outbreeding. This conclusion is based on the close agreement between observed and expected genotype frequencies in all the larger ($N > 30$) samples. This concordance is particularly impressive in the samples where four and five alleles are segregating at the Est-2 locus. In addition, estimates of inbreeding (F of Wright, 1965) and outcrossing (λ, where $F = (1 - \lambda/1 + \lambda)$, Nei and Syakudo, 1958) were also calculated for the four largest samples. In each case, lambda was greater than 0.96 thus confirming our conclusion regarding panmixia with respect to the allozymes studied.

The second important finding about *Cerion* was that like most other organisms

TABLE 12. VARIATION IN MALATE DEHYDROGENASES AND 6-PHOSPHOGLUCONATE DEHYDROGENASE.

Locality	Number of snails	Allele frequency					
		Mdh-1[a]	Mdh-1[b]	Mdh-2[a]	Mdh-2[b]	6-Pgdh[a]	6-Pgdh[b]
Grand Bahama—*C. bendalli*							
211	70	0.40	0.60	-----	1.00	0.64	0.36
208	1	1.00	-----	-----	1.00	1.00	-----
204B	64	0.65	0.35	-----	1.00	0.54	0.46
205	38	0.49	0.51	-----	1.00	0.67	0.33
207	6	0.50	0.50	-----	1.00	0.83	0.17
202	38	0.51	0.49	-----	1.00	0.64	0.36
200	6	0.42	0.58	-----	1.00	0.67	0.33
201	11	0.50	0.50	-----	1.00	0.68	0.32
Little Abaco—*C. bendalli*							
213	35	0.20	0.80	-----	1.00	1.00	-----
214	37	0.27	0.73	-----	1.00	1.00	-----
216	36	0.18	0.82	0.14	0.86	0.90	0.10
Great Abaco—*C. bendalli*							
217	18	0.28	0.72	0.08	0.92	1.00	-----
218	38	0.26	0.74	0.13	0.87	1.00	-----
224	45	0.32	0.68	0.01	0.99	1.00	-----
223	25	0.36	0.64	0.02	0.98	1.00	-----
222	39	0.35	0.65	0.03	0.97	1.00	-----
226	53	0.26	0.74	0.01	0.99	1.00	-----
220	56	0.25	0.75	-----	1.00	1.00	-----
219	77	0.36	0.64	-----	1.00	1.00	-----
316	14	0.43	0.57	-----	1.00	1.00	-----
228	21	0.36	0.64	0.05	0.95	1.00	-----
230	7	0.29	0.71	-----	1.00	1.00	-----
231	15	0.27	0.73	0.03	0.97	1.00	-----
240	37	0.28	0.72	-----	1.00	1.00	-----
247	37	0.34	0.66	-----	1.00	1.00	-----
243	102	0.29	0.71	-----	1.00	1.00	-----
245	42	0.31	0.69	-----	1.00	1.00	-----
244	41	0.37	0.63	-----	1.00	1.00	-----
Great Abaco—area of interaction between *C. bendalli* and *C. abacoense*							
260	36	0.28	0.72	-----	1.00	1.00	-----
501	12	0.33	0.67	-----	1.00	1.00	-----
308	24	0.21	0.79	-----	1.00	0.81	0.19
307	24	0.25	0.75	-----	1.00	0.69	0.31
306	36	0.31	0.69	-----	1.00	0.57	0.43
305	29	0.34	0.66	-----	1.00	0.53	0.47
304	36	0.29	0.71	-----	1.00	0.60	0.40
311	24	0.27	0.73	-----	1.00	0.56	0.44
253	36	0.39	0.61	-----	1.00	1.00	-----
255	30	0.35	0.65	-----	1.00	1.00	-----
251	84	0.43	0.57	-----	1.00	1.00	-----
Great Abaco—*C. abacoense*							
259	13	0.25	0.75	-----	1.00	0.62	0.38
520	7	0.36	0.64	-----	1.00	0.93	0.07
521	36	0.28	0.72	-----	1.00	0.40	0.60
254	34	0.29	0.71	-----	1.00	0.78	0.22
257	12	0.42	0.58	-----	1.00	0.75	0.25
252	24	0.25	0.75	-----	1.00	0.79	0.21
250	70	0.36	0.64	-----	1.00	1.00	-----

Table 13. Variation in glutamic oxalacetic transaminase and leucine aminopeptidase.

Locality	Number of Snails	Allele frequency					
		Got-1[a]	Got-1[b]	Got-1[c]	Lap-1[a]	Lap-1[b]	Lap-1[c]
Grand Bahama—*C. bendalli*							
211	70	0.67	0.33	.....	0.73	0.14	0.13
208	1	1.00	.....	.....	.....	1.00	.....
204B	64	0.77	0.23	.....	0.74	0.24	0.02
205	38	0.84	0.16	.....	0.78	0.17	0.05
207	6	0.33	0.67	.....	0.92	0.08	.....
202	38	0.55	0.45	.....	0.89	.....	0.11
200	6	0.58	0.42	.....	0.92	.....	0.08
201	11	0.47	0.53	.....	0.77	.....	0.23
Little Abaco—*C. bendalli*							
213	35	0.60	0.40	.....	0.81	.....	0.19
214	37	0.66	0.34	.....	0.86	.....	0.14
216	36	0.43	0.57	.....	0.96	.....	0.04
Great Abaco—*C. bendalli*							
217	18	0.56	0.44	.....	0.97	.....	0.03
218	38	0.54	0.46	.....	0.95	.....	0.05
224	45	0.51	0.49	.....	0.96	.....	0.04
223	25	0.56	0.44	.....	0.96	.....	0.04
222	39	0.59	0.41	.....	0.95	.....	0.05
226	53	0.48	0.52	.....	0.96	.....	0.04
220	56	0.46	0.54	.....	0.95	.....	0.05
219	77	0.51	0.49	.....	0.99	.....	0.01
316	14	0.54	0.46	.....	0.89	.....	0.11
228	21	0.50	0.50	.....	1.00	.....	.....
230	7	0.57	0.43	.....	1.00	.....	.....
231	15	0.53	0.47	.....	0.97	.....	0.03
240	37	0.55	0.45	.....	0.96	.....	0.04
247	37	0.58	0.42	.....	0.93	.....	0.07
243	102	0.47	0.53	.....	0.87	.....	0.13
245	42	0.54	0.46	.....	0.90	.....	0.10
244	41	0.52	0.48	.....	0.95	.....	0.05
Great Abaco—area of interaction between *C. bendalli* and *C. abacoense*							
260	36	0.58	0.42	.....	0.90	.....	0.10
501	12	0.54	0.46	.....	0.88	.....	0.12
308	24	0.50	0.42	.08	0.94	.....	0.06
307	24	0.69	0.31	.....	0.81	.....	0.19
306	36	0.56	0.44	.....	0.78	.....	0.22
305	29	0.57	0.43	.....	0.90	.....	0.10
304	36	0.60	0.40	.....	0.86	.....	0.14
311	24	0.44	0.54	0.02	0.90	.....	0.10
253	36	0.53	0.47	.....	0.67	0.14	0.19
255	30	0.48	0.50	0.02	0.72	0.13	0.15
251	84	0.51	0.47	0.02	0.83	0.04	0.13
Great Abaco—*C. abacoense*							
259	13	0.62	0.38	.....	0.81	.....	0.19
520	7	0.36	0.64	.....	0.50	.....	0.50
521	36	0.32	0.68	.....	0.82	.....	0.18
254	34	0.28	0.72	.....	0.73	0.09	0.18
257	12	0.58	0.42	.....	0.79	0.13	0.08
252	24	0.38	0.62	.....	0.77	.....	0.23
250	70	0.61	0.38	0.01	0.71	0.22	0.06

TABLE 14. VARIATION IN ESTERASE-2.

Locality	Number of Snails	Allele frequency						
		Est-2[a]	Est-2[b]	Est-2[c]	Est-2[d]	Est-2[e]	Est-2[f]	Est-2[g]
Grand Bahama—*C. bendalli*								
211	70	-----	-----	0.04	0.18	0.24	0.54	<0.01
208	1	-----	-----	-----	-----	1.00	-----	-----
204B	64	-----	-----	0.05	0.14	0.46	0.32	0.03
205	38	-----	-----	0.03	0.07	0.54	0.33	0.03
207	6	-----	-----	0.08	-----	0.42	0.42	0.08
202	38	-----	-----	0.01	0.20	0.14	0.58	0.07
200	6	-----	-----	-----	0.17	-----	0.83	-----
201	11	-----	-----	-----	0.23	0.09	0.68	-----
Little Abaco—*C. bendalli*								
213	35	-----	-----	-----	0.10	-----	0.90	-----
214	37	0.01	0.01	-----	0.22	-----	0.76	-----
216	36	-----	-----	-----	-----	-----	1.00	-----
Great Abaco—*C. bendalli*								
217	18	-----	-----	-----	0.22	-----	0.78	-----
218	38	-----	-----	-----	0.04	-----	0.96	-----
224	45	-----	-----	-----	0.06	-----	0.94	-----
223	25	-----	-----	-----	0.10	-----	0.90	-----
222	39	-----	-----	-----	0.03	-----	0.97	-----
226	53	-----	-----	-----	0.07	-----	0.93	-----
220	56	-----	-----	-----	0.02	-----	0.98	-----
219	77	-----	-----	-----	0.05	-----	0.95	-----
316	14	-----	-----	-----	0.04	-----	0.96	-----
228	21	-----	-----	-----	0.02	-----	0.98	-----
230	7	-----	-----	-----	0.14	-----	9.86	-----
231	15	-----	0.03	-----	0.10	-----	0.87	-----
240	37	-----	-----	-----	-----	-----	1.00	-----
247	37	-----	-----	-----	-----	-----	1.00	-----
243	102	-----	-----	-----	0.03	-----	0.97	-----
245	42	-----	-----	-----	-----	-----	1.00	-----
244	41	-----	-----	-----	-----	-----	1.00	-----
Great Abaco—area of interaction between *C. bendalli* and *C. abacoense*								
260	36	-----	0.03	-----	0.64	-----	0.33	-----
501	12	-----	0.04	-----	0.58	-----	0.38	-----
308	24	-----	0.02	-----	0.52	-----	0.46	-----
307	24	-----	0.08	-----	0.40	-----	0.52	-----
306	36	-----	-----	-----	0.29	-----	0.71	-----
305	29	-----	0.02	-----	0.26	-----	0.72	-----
304	36	-----	0.03	-----	0.57	-----	0.40	-----
311	24	-----	0.08	-----	0.54	-----	0.31	0.06
253	36	-----	0.09	-----	0.85	-----	0.06	-----
255	30	-----	0.10	-----	0.85	-----	0.05	-----
251	84	-----	-----	-----	-----	-----	1.00	-----
Great Abaco—*C. abacoense*								
259	13	-----	-----	-----	0.50	-----	0.50	-----
520	7	-----	-----	-----	-----	-----	1.00	-----
521	36	-----	-----	-----	0.19	-----	0.81	-----
254	34	-----	-----	-----	0.28	-----	0.72	-----
257	12	-----	0.04	-----	0.50	-----	0.46	-----
252	24	-----	-----	-----	0.25	-----	0.75	-----
250	70	-----	-----	-----	0.04	-----	0.96	-----

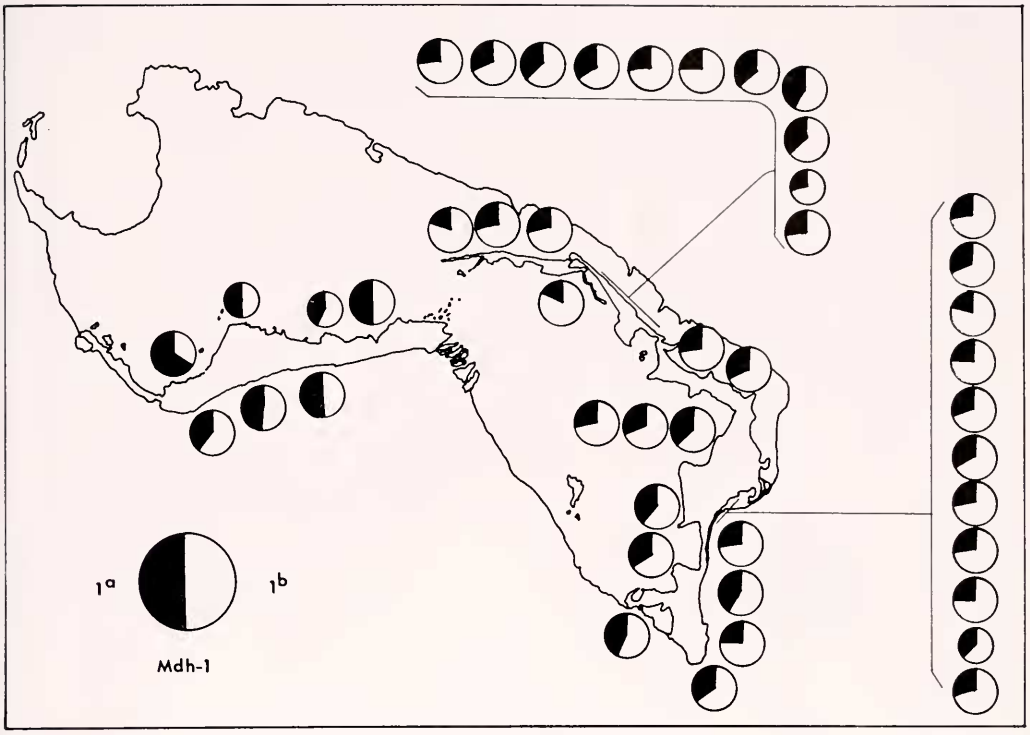

Figure 11. Geographic variation in malate dehydrogenase-1. Sample locality numbers may be discerned from Figure 3.

with open population structures, it has a rich endowment of genetic variability. The proportion of loci that are polymorphic per population (P) was in the range of 20–30 per cent (20–36 per cent if the variable but uninterpretable Est-3 and Pgi loci are included). Average heterozygosity per individual (H) was in the range of 5–12 per cent. Interpretation of variation in P and H will be discussed below after the geographic variation in the polymorphic allozymes has been described.

B. Geographic Variation in Polymorphic Loci

Having established that *C. bendalli* and *C. abacoense* were identical with respect to 14 genetic loci, we turned our attention to variation at the six polymorphic loci. We will present these data in two ways. In Tables 12–14, the allele frequencies are shown with the localities grouped according to geographic and taxonomic constraints. The decision as to whether a sample was placed in category 4 (transition zone) in the tables or in category 5 (*C. abacoense*) was based on shell morphology as outlined in the previous section. In Figures 11–16, the presentations are not biased by any a priori taxonomic constraints. Note that the smallest samples are not shown in the figures. We have initially resisted the temptation to group our samples according to island or sample region in any more formal sense, because the population structure of these animals suggests that such data pooling could seriously distort our conclusions.

Malate dehydrogenase-1. Two NAD dependent alleles have been demonstrated at this locus in *C. bendalli* from Abaco (Gould

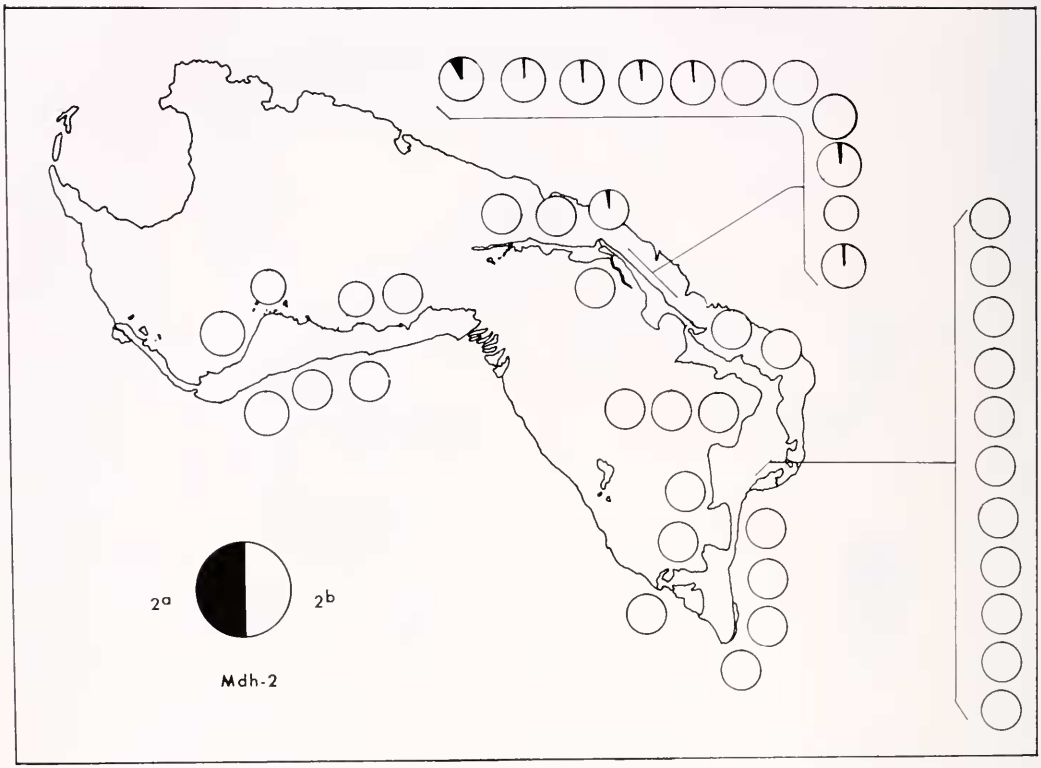

Figure 12. Geographic variation in malate dehydrogenase-2. Sample locality numbers may be discerned from Figure 3.

et al., 1974; Woodruff, 1975). Data in Table 12 and Fig. 11 indicate that there is no consistent difference in allele frequency between *C. bendalli* and *C. abacoense* morphotypes on Great Abaco where Mdh-1[a] varies in frequency between 0.21–0.43 in both taxa. Elsewhere, frequencies of Mdh-1[a] are slightly different: being lower on Little Abaco (0.18–0.27), and higher on Grand Bahama (0.40–0.65). Allele frequencies in adjacent populations are similar, and no dramatic shifts or clines in allele frequency were noted. There is no marked change in this allozyme in the area of interaction between *C. bendalli* and *C. abacoense* on Great Abaco.

Malate dehydrogenase-2. Gould et al. (1974) found two alleles at this locus in populations of *C. bendalli* from northern Great Abaco. NAD–Mdh-2[a] is a rare allele (0.01–0.04) that occurs in standard *C. bendalli* and in some samples of the aberrant Pongo Carpet morphotype found in this area. This allele was detected in populations extending from the eastern end of Little Abaco (Loc. 216) south to Treasure Cay, a distance of about 30 km. (It was not found in the three most isolated (and morphometrically differentiated) of the Pongo Carpet samples.) Subsequently, Woodruff (1975) reported Mdh-2[a] was absent in 3 samples of *C. bendalli* from localities about 50 km. south of this area. We now report that the Mdh-2[a] allele has not been detected in over 1,000 snails from elsewhere on the Little Bahama Bank (Table 12, Fig. 12). We conclude that *C. bendalli* and *C. abacoense* are not differentiated at

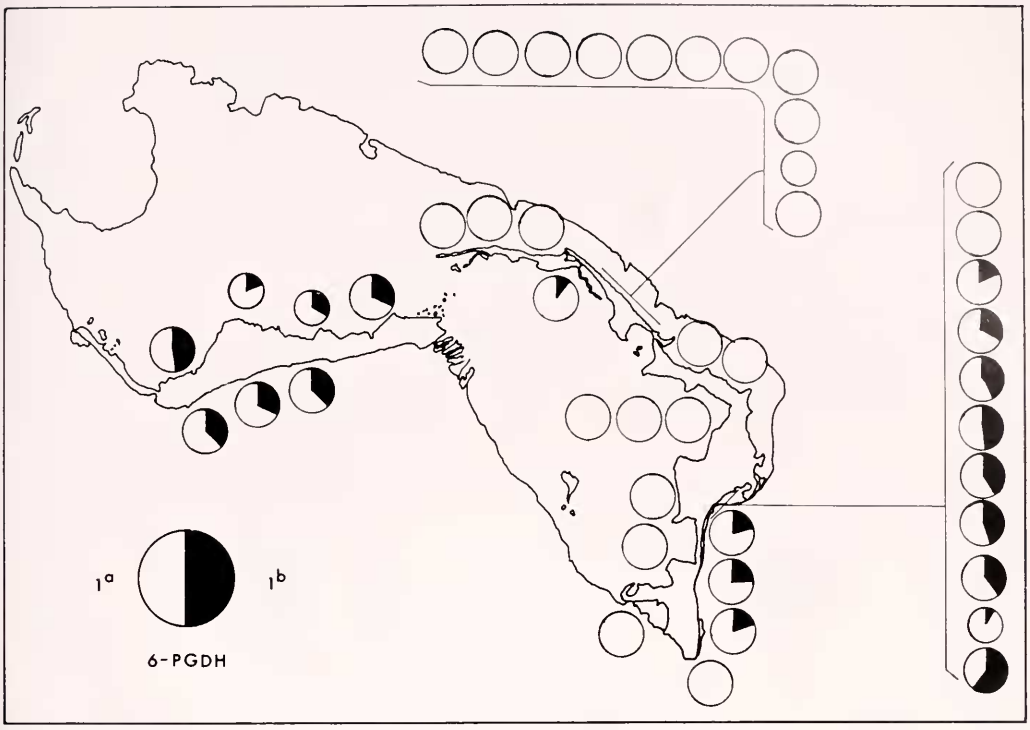

Figure 13. Geographic variation in 6-phosphogluconate dehydrogenase. Sample locality numbers may be discerned from Figure 3.

this locus and that the presence of the rare allele in northern Great Abaco is a biochemical area effect. Until more is known about the variation of this gene elsewhere in the Bahamas, we are inclined to invoke mutation and the spread of a locally advantageous allele as the most likely explanation for this phenomenon. An alternative hypothesis—that Mdh-2ª was introduced into the area with the aberrant Pongo Carpet morphotype by hurricane transport from elsewhere—is rejected at present because the allele was not detected in the three most differentiated populations of the Pongo Carpet snails.

6-Phosphogluconate dehydrogenase. While populations of *C. bendalli* from near Pongo Carpet (Gould et al., 1974) and Snake Cay, Great Abaco (Woodruff, 1975) are monomorphic for 6-Pgdhª, a second codominant allele (6-Pgdh-1ᵇ) has been found elsewhere on the Little Bahama Bank (Fig. 13). This allozyme stains as a single, sharp band of slightly reduced mobility relative to 6-Pgdh-1ª; heterozygotes are 3-banded. As shown in Table 11 and Fig. 13, all samples from Grand Bahama are polymorphic with 6-Pgdh-1ª varying in frequency between 0.54–0.83. On Little and Great Abaco, the 6-Pgdh-1ᵇ allele has been found in two separate areas. First, at the eastern end of Little Abaco (Loc. 216), 7 heterozygotes were noted among 36 snails examined. No trace of this allele was found in the sample from Loc. 217 which was collected 100 m away on Great Abaco at the other end of the causeway connecting the two islands. Sixty kilometers further south, the 6-Pgdh-1ᵇ allele was found again in samples from the area of interaction between *C. bendalli* and *C. abacoense*. It was detected in 6 of 11 samples between Rocky

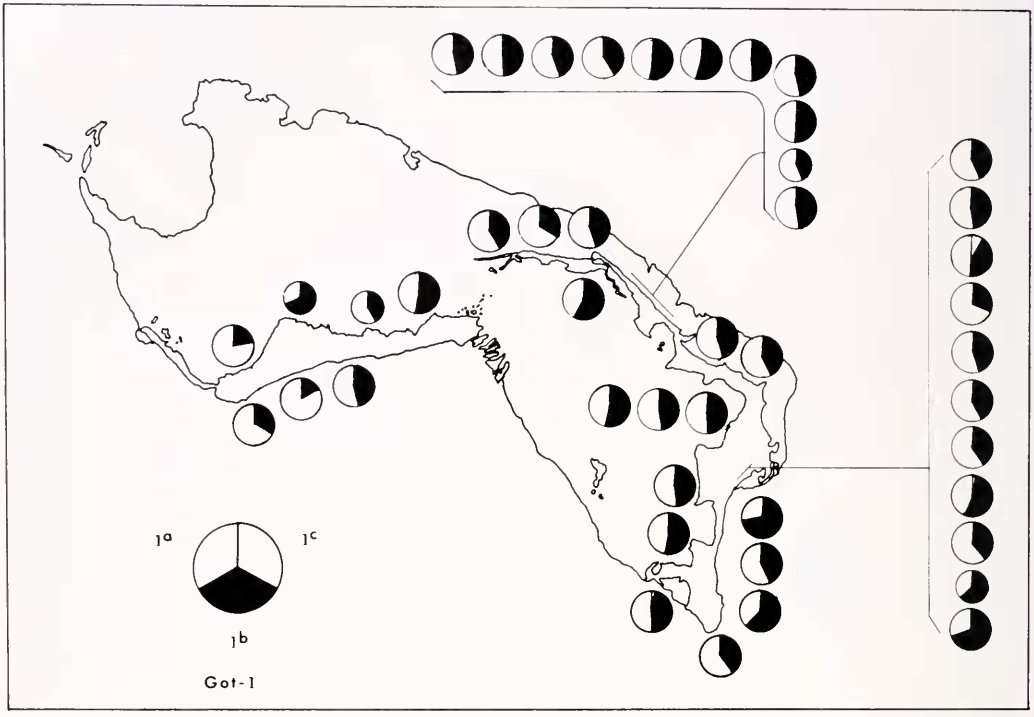

Figure 14. Geographic variation in glutamic oxalacetic transaminase. Sample locality numbers may be discerned from Figure 3.

Point and The Crossing and in 5 of 6 samples of *C. abacoense* morphotype. Its frequency in this area ranged up to 0.60 in the populations where it was detected. It was, however, conspicuously absent in samples of intermediate morphotype from the west side of The Crossing (Locs. 253, 255) and Sandy Point (Loc. 251) and in the "pure" *C. abacoense* from Hole-in-the-Wall (Loc. 250). The isolated occurrence of 6-Pgdh-1^b on Little Abaco is tentatively interpreted as being due to mutation and drift. The occurrence of this allele at higher frequencies on Grand Bahama and in the transition zone between the morphotypes on Great Abaco must be due to other forces.

Glutamic oxalacetic transaminase. In *C. bendalli*, two equally common alleles were found in 12 populations from northern and central Great Abaco (Gould et al., 1974; Woodruff, 1975). As seen in Table 13 and Fig. 14, Got-1^a occurs at a slightly higher frequency than Got-1^b throughout the range of this taxon. Got-1^a reaches its greatest frequencies (0.77–0.84) in western and interior samples from Grand Bahama. Seven samples of the ribby morphotype, *C. abacoense*, were also examined and found to have Got-1^a frequencies of 0.28–0.62. Frequencies of 0.44–0.69 were found to characterize samples from the area of interaction between these taxa. A third allele, Got-1^c is now reported from southern Great Abaco where it occurs at low frequency (0.01–0.08). It has been detected in "pure" *C. abacoense* (Loc. 250) and 4 samples of intermediate morphotype from Sandy Point (Loc. 251), The Crossing (Loc. 255) and near Rocky Point (Locs. 308, 311). This rare allele has yet to be found in "pure" *C. bendalli* from Abaco or Grand Bahama. In mobility, Got-1^c is slower than Got-1^b;

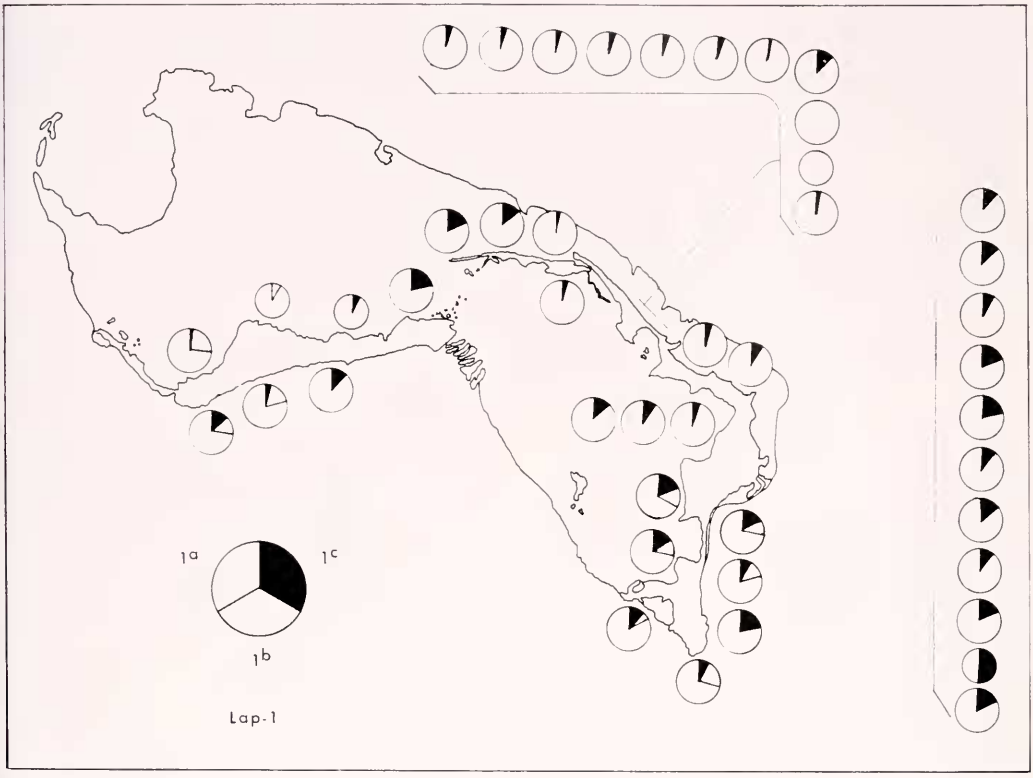

Figure 15. Geographic variation in leucine aminopeptidase. Sample locality numbers may be discerned from Figure 3.

like the latter the former stains a well-defined doublet, the heterozygotes having four bands.

Leucine aminopeptidase. We have previously shown that Lap-1^a is the predominant allele in *C. bendalli* near Pongo Carpet and Snake Cay (Gould et al., 1974; Woodruff, 1975). In these populations a slower allele (previously designated Lap-1^b) occurred at a frequency of up to 0.13. Now we report finding a third allele of intermediate mobility in *Cerion* from Grand Bahama and southern Great Abaco (Table 13, Fig. 15). For consistency, the newly discovered allele is now designated Lap-1^b; the designation of the slowest allele is accordingly changed to Lap-1^c.

Lap-1^a is the common allele throughout the Little Bahama Bank: it varies in frequency and is typically over 0.85 (range: 0.67–1.00). Lap-1^c is also widespread. Its absence in a few samples is presumably due to sampling error. No particular biological significance is attached to the minor interpopulation variation in frequency of this allele. The third allele, Lap-1^b, is known from 5 localities in western Grand Bahama and from 6 localities at the southern end of Great Abaco. It reaches its highest frequency in the interior of the pine forest on Grand Bahama and in "pure" *C. abacoense* from Hole-in-the-Wall on Great Abaco. Lap-1^b was detected from 4 to 5 localities at The Crossing where it has a frequency of about 0.10.

Esterase-2. Woodruff (1975) first detected variation at this non-specific esterase locus in *C. bendalli* from Loc. 243 near

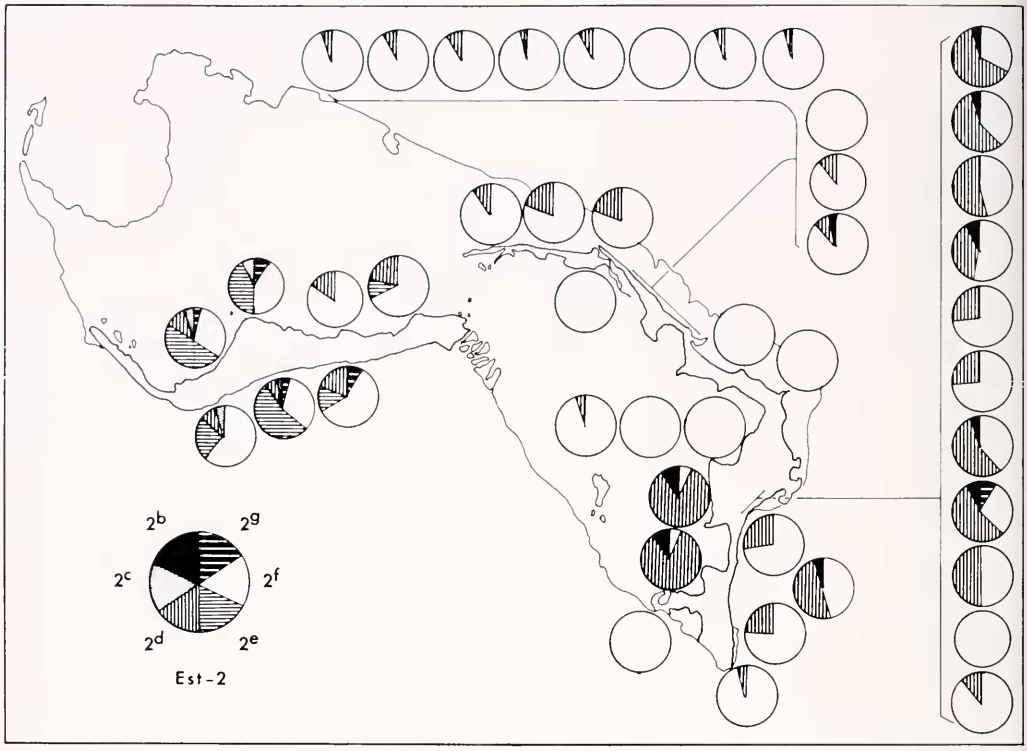

Figure 16. Geographic variation in esterase-2. Sample locality numbers may be discerned from Figure 3.

Snake Cay, Great Abaco. At that time, the codominant alleles were designated Est-2^b and Est-2^c. Now, as a result of this far more extensive survey, we report that at least 7 alleles occur at this locus among the *Cerion* of the Little Bahama Bank. The various alleles are all codominant and are designated Est-2^a, Est-2^b . . . Est-2^g in order of decreasing mobility. The alleles reported by Woodruff (1975) are now redesignated Est-2^d and Est-2^f respectively. Allele frequencies and the overall pattern of allele distribution are shown in Table 14 and Fig. 16. Est-2^a, a very rare allele found in only one sample, is omitted from Fig. 16. The distribution of each allele may now be considered in turn.

Est-2^a. A rare allele whose presence is based on a single specimen of *C. bendalli* from Little Abaco with a two-banded phenotype interpreted as Est-2^a/Est-2^f.

Est-2^b. Another rare allele found in 12 samples of *C. bendalli* from Great and Little Abaco. Its isolated occurrence on Little Abaco and near Treasure Cay may be due to recurrent mutation. Its occurrence at frequencies of up to 0.10 in ten samples from the area of interaction between *C. bendalli* and *C. abacoense* is probably due to other forces. We note that nine of these samples were of *C. bendalli* or intermediate morphotype; only one (Loc. 257 at The Crossing) was referable to *C. abacoense*. In this same area, the Est-2^b allele was not detected at Locs. 259, 520, 521, 254, and 252 where snails are judged to be typical *C. abacoense*.

Est-2^c. A rare allele (frequency: 0.01–0.8) detected in heterozygous form in four populations of *C. bendalli* from western Grand Bahama.

Est-2^d. A common allele detected in most populations of *Cerion* from the Little Ba-

hama Bank. It occurs at moderate frequencies (0.02–0.23) throughout most of the range of the *C. bendalli* morphotype. The notable feature about the distribution of this allele is that it reaches higher frequencies in the area of interaction between the two morphotypes on Great Abaco than elsewhere. In fact, it is the commonest allele at eight localities in this area. Intersample variation in this area is also marked and is probably too great to be due to sampling error alone. For example, Est-2^{d} occurs at the three localities on the eastern side of The Crossing at frequencies of 0.25–0.50 while on the western side of The Crossing, only 500 m away, the allele is present at a frequency of 0.85 in two localities. The absence of Est-2^{d} at Sandy Point (Loc. 251) is probably not due to sampling error.

Est-2^{d} is also present throughout northern Great Abaco although its presence in some populations was not detected by Gould et al. (1974). We have subsequently rerun all the Pongo Carpet specimens and now report the occurrence of this allele at low frequency. This correction does not alter any of the conclusions we reached in that paper about the systematic status of the Pongo Carpet morphotype.

Est-2^{e}. This allele was detected on Grand Bahama where it occurs in all populations sampled (its absence at Loc. 200 is almost surely due to sampling error) and is the commonest allele in the three interior samples.

Est-2^{f}. This is the commonest allele in the majority of the *Cerion* populations on the Little Bahama Bank. It varies in frequency between 0.76–1.00 in samples of *C. bendalli* from Little Abaco and Great Abaco. It is less common in *C. bendalli* from Grand Bahama where it falls to frequencies as low as 0.32–0.42 in the interior populations dominated by Est-2^{e}. Lower frequencies were also noted in the area of interaction between *C. bendalli* and *C. abacoense* where Est-2^{d} was the commonest allele in 7 of 11 samples. This area and the adjacent populations of *C. abacoense* is also characterized by considerable interpopulation variation in the frequency of Est-2^{f}. This is particularly marked at The Crossing where the frequency of Est-2^{f} increases from 0.05–0.06 in the mottled western samples to 0.46–0.75 in the ribby eastern samples.

Est-2^{g}. A rare allele occurring at low frequency in five samples of *C. bendalli* from Grand Bahama and one sample of intermediate morphotype from Great Abaco.

C. Genetic Differentiation of *Cerion* on the Little Bahama Bank

The patterns of geographic variation in the six polymorphic enzymes bear little relation to the distribution of the two taxa recognized on the basis of shell morphology. There is not a single case of fixation, or even near fixation, for alternative alleles in the two taxa. In only 5 out of the 19 polymorphic cases is an allele restricted to one or the other morphotype: Est-2^{a}, Est-2^{c}, Est-2^{e}, Est-2^{g}, and Mdh-2^{a}. With the exception of Est-2^{e}, which is common in the interior of Grand Bahama, these alleles are all rare in most or all of the samples in which they were detected. The overall impression emerging from these data is that *C. bendalli* and *C. abacoense* are very similar to one another genically. This conclusion was confirmed by calculating the normalized identity of genes (*I* of Nei, 1972) between all 41 samples where $N > 11$. The values of *I* obtained for the 820 pairwise combinations of samples were in the range 0.9451–0.9999. The average similarity was 0.9849. Values of Nei's (1972) genetic distance, *D*, were accordingly very small and do not exceed 0.0564.

This overall lack of pronounced genetic differentiation does not mean that local patterns of variation cannot be discerned. On the contrary we find sporadic occurrences of alleles that are unique to one group of populations or another. There is also a moderate amount of interpopulation variation that does not appear to be either obviously clinal or closely correlated with simple environ-

TABLE 15. VALUES OR MEAN VALUES FOR NEI'S GENETIC DISTANCE (*D*) BETWEEN VARIOUS SAMPLES OR GROUPS OF SAMPLES (N) OF *Cerion bendalli* FROM GRAND BAHAMA (G.B.) AND *Cerion* FROM ELSEWHERE ON THE LITTLE BAHAMA BANK. MORPHOTYPES ARE B (*C. bendalli*), Ab (*C. abacoense*) AND I (INTERMEDIATE). NOTE PARTICULARLY THE ACROSS-TABLE LOW VALUES FOR COMPARISONS INVOLVING ROCKY POINT AND THE CROSSING—EAST, AND HIGH VALUES FOR COMPARISONS INVOLVING THE CROSSING—WEST.

			Grand Bahama Sample				
Sample(s)	Morph	N	211	204	205	202	201
Loc. 211, G.B.	B	1	—	—	—	—	—
Loc. 204, G.B.	B	1	.0082	—	—	—	—
Loc. 205, G.B.	B	1	.0066	.0032	—	—	—
Loc. 202, G.B.	B	1	.0033	.0120	.0129	—	—
Loc. 201, G.B.	B	1	.0051	.0184	.0195	.0018	—
Little Abaco	B	3	.0161	.0422	.0329	.0157	.0134
Pongo Carpet	B	9	.0170	.0411	.0332	.0142	.0124
Treasure Cay	B	2	.0176	.0414	.0336	.0143	.0128
Snake Cay	B	3	.0180	.0428	.0350	.0151	.0123
Rocky Point	I	6	.0082	.0250	.0233	.0076	.0083
The Crossing—east	Ab	3	.0101	.0304	.0285	.0083	.0056
The Crossing—west	B	2	.0301	.0440	.0417	.0308	.0299
Sandy Point	I	1	.0170	.0389	.0332	.0141	.0107
Hole-in-the-Wall	Ab	1	.0146	.0356	.0292	.0162	.0154

mental parameters. Regional differentiation is most marked for the Grand Bahama populations. These are distinguishable from Abaconian populations on the basis of their higher frequencies of Mdh-1^a and Lap-1^b and lower frequency of 6-Pgdh-1^a. This differentiation does not, however, permit the characterization of individual specimens. Only in Est-2 has any regional differentiation of diagnostic genotypes occurred: Est-2^c and Est-2^e are restricted to Grand Bahama, while Est-2^a and Est-2^b have been detected only on Abaco. A second potentially diagnostic allele may be Got-1^c found in *C. abacoense* and populations of intermediate morphotype on southern Great Abaco. It is regrettable that we do not know, at this time, whether Got-1^c characterizes *C. abacoense* from Mores Island or whether it was present in the presumed extinct *C. abacoense* from Grand Bahama. Indeed *C. abacoense* cannot be considered properly characterized until more samples away from the area of interaction with *C. bendalli* have been analyzed.

We are struck by the similarity between populations of *C. bendalli* on Grand Bahama and populations of *Cerion* from the area of interaction on Great Abaco. This pattern emerged repeatedly in the distribution of individual alleles: 6-Pgdh-1^b, Lap-1^b, and Est-2^g (Figures 13, 15, 16). It is also apparent from a comparison of interpopulation genetic distances (Table 15). In each set of interpopulation distance comparisons, we see that Grand Bahamian populations are more similar to Abaconian populations from the eastern side of the area of interaction between *C. bendalli* and *C. abacoense* than they are to Abaconian *Cerion* of either taxon collected away from this area. This pattern is consistent and not obscured by the slight regional differentiation on Grand Bahama itself. Note also that *D* values between the populations on either side of The Crossing are greater than those between various isolated populations of *C. bendalli* and greater than those between the "parental" taxa themselves.

This similarity between *Cerion* from Grand Bahama and the area of interaction on Abaco was noted again in the pattern of variation for individual heterozygosity (*H*). Table 16 shows that significantly higher levels of heterozygosity prevail in these two areas than elsewhere on the Little Bahama

Bank. In this case, however, populations on both sides of The Crossing are characterized by higher values of *H*.

Although we treat the determinants of these patterns more fully elsewhere (Woodruff and Gould, in prep.), we can make some general comments about their relationship to ecology and genetics of *Cerion*. *Cerion* populations are very variable in size. While Woodruff's study demes are moderate (N = approx. 1,000) in size and contiguous with adjacent demes, this is not always the case. *Cerion*'s distribution is typically patchy, and dramatic declines in abundance occur over a distance of a few meters. Stochastic processes are undoubtedly important in small, isolated populations. Gene flow is restricted by the low vagility of the snails themselves but is nevertheless demonstrable in nature. Recurrent mutation is probably responsible for some aspects of genic variation in Little Bahama Bank *Cerion*. Finally, selection may play an important role in regulating the frequency of certain alleles, either directly or through its action on coadapted, linked gene complexes.

It is likely that these various stochastic and deterministic agents act differentially on the various populations which differ in size and degree of isolation or exposure to gene flow. In this context it may be recalled that we found moderate amounts of genic variability in *Cerion*: mean number of alleles per locus lies in the range 1.65–1.70, frequency of loci polymorphic per population ranged from 0.15–0.30, and the frequency of heterozygous loci per individual ranged from 0.054–0.128. The occurrence of more variable populations in some areas may indicate greater environmental heterogeneity or perhaps increased levels of gene flow between partially differentiated populations. Alternatively, lower levels of genic variation elsewhere may indicate environmental homogeneity and reduced levels of gene flow. It must be remembered, however, that higher (or lower) levels of variability in different areas (as in the case of

Table 16. Genic heterozygosity (H) per individual for various samples and groups of samples (N) of *Cerion* from the Little Bahama Bank.

Sample(s)	N	$\bar{H}$	(range)
Grand Bahama	7	10.43	(9.17–12.27)
Little Abaco	3	6.25	(6.22–6.28)
Pongo Carpet	9	6.01	(5.67–6.67)
Treasure Cay	3	5.30	(4.52–5.71)
Snake Cay	3	5.37	(5.00–5.74)
Rocky Point	7	10.46	(8.95–11.50)
The Crossing—east	3	9.63	(8.30–10.60)
The Crossing—west	2	9.35	(9.03–9.67)
Sandy Point	1	6.40	—
Hole-in-the-Wall	1	7.00	—

Cerion from Grand Bahama and The Crossing on Great Abaco) may have quite different determinants. Thus, while the overall pattern of genic variation in these *Cerion* may appear relatively simple, we should be alert for the selective development of slightly different coadapted gene complexes in different areas. As in the case of an area effect in *Cepaea nemoralis* recently restudied by Johnson (1976), we expect much synergism between history, environmental selection, and coadaptation.

Finally, we note that the overall genic similarity of *Cerion* on Little Bahama Bank indicates that these populations were not founded by dozens of independently derived hurricane-borne propagules. While we cannot exclude the possibility of hurricane transport of alleles from elsewhere, we cannot properly assess the significance of such occurrence until we have completed our survey of genic variation elsewhere in the Bahamas and Cuba. Until this information is gathered, we prefer to interpret the pattern of genic variation as a product of evolution *in situ*, probably during Pleistocene hypothermals when the Little Bahama Bank was a single large island. The differentiation between Grand Bahama and Abaco could easily have occurred since the flooding of the bank, when the various island populations became isolated from each other. Using Nei's (1975) crude but useful method of relating electrophoretic

data to time of evolutionary divergence, where $t = 5 \times 10^5 D$ (and taking 0.0150 for D), we find that the Grand Bahamian and Abaconian populations diverged about 7,500 years ago if rates of genetic change have been constant. This is very close to the estimated time of submergence for the bank.

V. DISCUSSION

The preceding genic analysis has considerable bearing on the taxonomic status of ribby and mottled morphotypes. We have shown that patterns of allozyme variation bear little relation to distribution of the shell morphotypes. In fact, these taxa are so similar to one another that if we had never seen samples from the area of interaction, we would probably have concluded that the two morphotypes are genically identical. Recall that the highest value of D calculated among 820 comparisons was only 0.0564 ($I = 0.9451$). The degree of genic differentiation found among 47 populations of *Cerion* on Little Bahama Bank is well within the limits found among conspecific populations of comparable land snails. Greater interpopulation variation has been detected among the *Helix aspersa* inhabiting two adjacent city blocks in Bryan, Texas (Selander and Kaufman, 1975), among eight populations of *Theba pisana* in Israel (Nevo and Bar, 1976), and among ten populations of *Cepaea nemoralis* in North America (Brussard, 1975). As a generalization emerging from a rapidly increasing number of studies, comparison of local populations typically produces values of D in the range 0.001–0.01, while subspecific comparisons exhibit $D = 0.004$–0.351, and specific comparisons yield $D = 0.05$–2.73 (Nei, 1975). In the *willistoni* group of *Drosophila*, for example, average values of D are: 0.03 between geographic populations; 0.23 between subspecies and semispecies; and 0.66 between sibling species (Ayala, 1975). Clearly, on the basis of these generalizations, we should synonymize *C. bendalli* with *C. abacoense* and treat the Little Bahama Bank *Cerion* as a single variable species. We choose not to do this for several reasons.

First, variation in structural gene products tells us nothing, *per se*, about the development of reproductive isolation. Although a large number of allelic substitutions usually precede the completion of reproductive isolation (typically about 20 per 100 loci (Ayala, 1975)), there are many exceptions. Species pairs characterized by very low values of D include *Drosophila persimilis* and *D. pseudoobscura*, 0.05 (Prakash, 1969); *Thomomys bottae* and *T. umbrinus*, 0.009–0.054 (Patton et al., 1972; Patton, 1973); and the semispecies of *Drosophila paulistorum*, 0.025 (Richmond, 1972). At the other extreme, levels of genic divergence are similar between various sibling species of *Drosophila*, 0.67 (Ayala, 1975); humans and chimpanzees, 0.62 (King and Wilson, 1975); and local populations of a pocket gopher *Geomys bursarius*, (Rogers' $D =$ 0.65–0.89) (Penney and Zimmerman, 1976). Values of D do not by themselves permit us to make unequivocal taxonomic decisions.

Secondly, the genic and morphometric surveys, taken together, both indicate that something notable is going on in the area of interaction between morphotypes. Although we find no increased variability in shell form, *Cerion* from this area are significantly more variable genically than samples collected elsewhere. They are polymorphic for alleles not found in either adjacent "parental" population (6-Pgdh-1^b and Est-2^b). A similar phenomenon was discovered in the hybrid zone between *Mus musculus musculus* and *M.m. domesticus* in Denmark (Hunt and Selander, 1973). Populations in this area also display higher levels of P and H, as well as increased intersample variation. This is particularly marked at The Crossing where between morphotype gene flow is presumably restricted by an intervening hill. Average values of D between samples on the east and west side of the hill are 0.0068 and 0.0003 respectively; D values between sam-

ples on either side of the hill average 0.0235. We tentatively interpret this situation as an interaction between two partially differentiated taxa possessing slightly different coadapted genc complexes.

Moreover, on New Providence Island, the same two morphotypes (under different names) interact to yield a "classic" hybrid zone, with unique phenotypes and greatly increased morphological variability in the intermediate samples. In fact, wherever the two morphotypes interact in the Bahamas (and they do on several islands), the hybrid zones are marked and narrow. We have never failed to find some evidence—either morphological (as on New Providence) or genetic (as on Abaco and in partly completed studies of several zones on Long Island)—of abrupt change, marked discontinuity, or greatly increased variability. The two morphotypes never blend evenly, and we take this as a sign that their mixtures involve two at least moderately discordant entities. We believe that this discordance deserves some taxonomic recognition above the subspecific level. The morphotypes are not mere geographic variants. (Simple geographic variants do abound as well; we designate as such the Pongo Carpet samples of *C. bendalli* because their morphological transitions to normal populations are smooth and because they share with adjacent samples of normal *C. bendalli* a genetic anomaly peculiar to their region—see Gould et al., 1974.) Structural gene products, in any case, do not control the alteration of developmental (allometric) rates that lie at the core of differences between morphotypes of *Cerion*. We shall have to learn how to study the genetics of eukaryotic regulation before the fundamental problems of *Cerion* are resolved.

Finally, we are now studying a series of hybrid zones involving *Cerion* of radically different morphology elsewhere in the Bahamas. Our preliminary electrophoretic surveys suggest that some of the most distinctive morphotypes (recognized as separate subgenera) of *Cerion* have differentiated to a lesser extent than semispecies in groups like *Drosophila willistoni*. Until we know more about genic variation in *Cerion* as a whole, we will treat the mottled and ribby morphotypes as semispecies. Until we know more about them and their interactions (repeated under the guise of many different species names throughout the Bahamas and Cuba), we will recognize *C. bendalli* and *C. abacoense* as taxonomic species. In doing so we heed Lewontin's (1974) closing dictum that "context and interaction are of the essence."

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REFERENCES CITED

Avise, J. C. 1974. Systematic value of electrophoretic data. Syst. Zool., **23**:465–481.

Ayala, F. J. 1975. Genetic differentiation during the speciation process. Evolutionary Biol., **8**:1–78.

Ayala, F. J. (ed.). 1976. Molecular Evolution. Sinauer Assoc., Sunderland, Mass., 277 pp.

Baker, H. B. 1924. Land and freshwater mollusks of the Dutch Leeward Islands. Occas. Pap. Mus. Zool. Univ. Mich., No. 152, 158 pp.

Bartsch, P. 1920. Experiments in the breeding of cerions. Carnegie Inst. Wash. Publ. 282, 59 pp., 59 plates.

Bartsch, P. 1931. Report on Cerion colonies planted on Florida Keys. Yearbook Carnegie Inst. Wash. **30**:373–378.

Brussard, P. F. 1975. Geographic variation in North American colonies of *Cepaea nemoralis*. Evolution **29**:402–410.

Burch, J. B. and D. C. Kim. 1962. Chromosomes of *Cerion incanum* (Binney) (Mollusca; Gastropoda: Stylommatophora). Bull. nat. Inst. Health (Korea) **5**:181–186.

Clench, W. J. 1935. A new species of *Cerion*

from Long Island, Bahamas, and a note on *Cerion milleri* (Pfeiffer). Nautilus **49**:49–50.

Clench, W. J. 1938. Land and freshwater mollusks of Grand Bahama and the Abaco Islands, Bahama Islands. Mem. Soc. Cubana Hist. Nat. **12**:303–333.

Clench, W. J. 1957. A catalogue of the Cerionidae (Mollusca-Pulmonata). Bull. Mus. Comp. Zool. **116**:121–169.

Dall, W. H. 1905. Fossils of the Bahama Islands, with a list of the non-marine mollusks. In G. B. Shattuck (ed.), The Bahama Islands. N.Y., MacMillan, pp. 23–47.

Endler, J. A. 1977. Geographic variation, speciation and clines. Princeton, New Jersey, Princeton Univ. Press.

Gould, S. J. 1969. Character variation in two land snails from the Dutch Leeward Islands: geography, environment and evolution. Syst. Zool. **18**:185–200.

Gould, S. J. 1971. The paleontology and evolution of *Cerion* II: age and fauna of Indian shell middens on Curaçao and Aruba. Breviora Mus. Comp. Zool. **372**: 26 pp.

Gould, S. J. and C. Paull. 1977. Natural history of Cerion VII: geographic variation of *Cerion* (Mollusca: Pulmonata) from the eastern end of its range (Hispaniola to the Virgin Islands): coherent patterns and taxonomic simplification. Breviora Mus. Comp. Zool. No. 445, 24 pp.

Gould, S. J., D. S. Woodruff, and J. P. Martin. 1974. Genetics and morphometrics of *Cerion* at Pongo Carpet: a new systematic approach to this enigmatic land snail. Syst. Zool., **23**: 518–535.

Heath, D. J. 1975. Colour, sunlight and internal temperatures in the land snail *Cepaea nemoralis* (L.). Oecologia **19**:29–38.

Hunt, W. G. and R. K. Selander. 1973. Biochemical genetics of hybridization in European house mice. Heredity, **31**:11–33.

Jaenicke, J. H. 1933. Untersuchungen zur Anatomie und Verschiedenartigkeit der *Cerion* Arten der Bahamas als Beitrag zum Problem der Artentstehung. Jena Z. Med. Naturwiss. **68**:277–402.

Johnson, M. S. 1976. Allozymes and area effects in *Cepaea nemoralis* on the western Berkshire Downs. Heredity **36**:105–121.

Johnston, R. F. 1975. Coincidences of genetic and phenetic variation in the house sparrow. In G. F. Estabrook (ed.), Proc. 8th Int. Conf. Numerical Taxonomy. San Francisco, W. H. Freeman, pp. 333–353.

King, M. C. and A. C. Wilson. 1975. Evolution at two levels. Molecular similarities and biological differences between humans and chimpanzees. Science **188**:107–116.

Klovan, J. E. and J. Imbrie. 1971. An algorithm and FORTRAN-IV program for large-scale Q-mode factor analysis and calculation of factor scores. Math. Geol. **3**:61–77.

Lamotte, M. 1951. Recherches sur la structure génétique des populations naturelles de *Cepaea nemoralis* (L.). Bull. Biol. Suppl. **35**: 1–239.

Lee, P. J. 1969. FORTRAN-IV Program for canonical correlation and canonical trend-surface analysis. Univ. Kansas, State Geol. Surv., Computer Contr. No. 32, 46 pp.

Lewontin, R. C. 1974. The Genetic Basis of Evolutionary Change. New York, Columbia Univ. Press, 346 pp.

Marcus, L. F. and J. H. Vandemeer. 1966. Regional trends in geographic variation. Syst. Zool. **15**:1–13.

May, R. M., J. A. Endler, and R. E. McMurtie. 1975. Gene frequency clines in the presence of selection opposed by gene flow. Amer. Nat. **109**:659–676.

Maynard, C. J. and N. A. Clapp. 1919–1926. Contributions to the history of the Cerionidae, with descriptions of many new species and notes on evolution in birds and plants. Appendix to Vol. 10, Records of Walks and Talks with Nature, West Newton, Mass., 242 pp.

Mayr, E. 1954. Change in genetic environment and evolution. In: Evolution as a Process, J. Huxley, A. C. Hardy, and E. B. Ford (eds.), pp. 188–213.

Mayr, E. 1963. Animal species and evolution. Cambridge, Mass., Harvard Univ. Press, 797 pp.

Mayr, E. 1976. Evolution and the diversity of life. Cambridge, Mass., Harvard Univ. Press, 721 pp.

Mayr, E. and C. B. Rosen. 1956. Geographic variation and hybridization in populations of Bahama snails (*Cerion*). Novitates Am. Mus. Nat. Hist. No. 1806, 48 pp.

Nei, M. 1972. Genetic distance between populations. Amer. Natur. **106**:283–292.

Nei, M. 1975. Molecular Population Genetics and Evolution. New York, American Elsevier.

Nei, M. and K. Syakudo. 1958. The estimation of outcrossing in natural populations. Jap. J. Genet. **33**:46–51.

Nevo, E. and Z. Bar. 1976. Natural selection of genetic polymorphisms along climatic gradients. In: Karlin, S. and E. Nevo (eds.), Population Genetics and Ecology. New York, Academic Press.

Patton, J. L. 1973. An analysis of natural hybridization between the pocket gopher *Thomomys bottae* and *Thomomys umbrinus* in Arizona. J. Mammal. **54**:561–584.

Patton, J. L., R. K. Selander, and M. H. Smith. 1972. Genic variation in hybridizing popula-

tions of gophers (genus *Thomomys*). Syst. Zool. **21**:263–270.

Penney, D. F. and E. G. Zimmerman. 1976. Genic divergence and local population differentiation by random drift in the pocket gopher genus *Geomys*. Evolution **30**:473–483.

Pilsbry, H. A. 1902. Family Cerionidae. Manual of Conchology, Second Series, Pulmonata, Vol. 14. Philadelphia, Acad. Nat. Sci., pp. 174–281.

Pilsbry, H. A. and E. G. Vanatta. 1895. New species of the genus *Cerion*. Proc. Acad. Nat. Sci. Philadelphia, pp. 206–210.

Pilsbry, H. A. and E. G. Vanatta. 1896. Catalogue of the species of *Cerion*, with descriptions of new forms. Proc. Acad. Nat. Sci. Philadelphia, pp. 315–338.

Plate, L. 1906. Die Artbildung bei den Cerion-Landschnecken der Bahamas. Verhandl. deutsch. Zool. Ges., pp. 127–136.

Plate, L. 1907. Die Variabilität und die Artbildung nach dem Prinzip geographischer Formenketten bei den *Cerion*-Landschnecken der Bahama-Inseln. Arch. Rassen Gesellsch. Biol. **4**:433–470, 581–614.

Prakash, S. 1969. Genetic variation in a natural population of *Drosophila persimilis*. Proc. Nat. Acad. Sci. USA **62**:778–784.

Rensch, B. 1932. Über die Abhängigkeit der Grösse, des relativen Gewichtes und der Oberflächenstruktur der Landschneckenschalen von den Umweltsfaktoren. Z. Morph. Ökol. Tiere **25**:757–807.

Reyment, R. A. 1975. Analysis of a generic level transition in Cretaceous ammonites. Evolution **28**:665–676.

Richmond, R. C. 1972. Enzyme variability in the *Drosophila willistoni* group. III. Amounts of variability in the superspecies *D. paulistorum*. Genetics **71**:87–112.

Richter, K. 1926. Zur Anatomie von *Cerion glans* Küster der Bahamas-Inseln. Jena Z. Med. Naturwiss. **62**:277–342.

Schmidt-Nielson, K., Taylor, C. R., and A. Shkolnik. 1971. Desert snails: problems of heat, water, and food. J. Exp. Biol. **55**:385–398.

Selander, R. K. and R. O. Hudson. 1976. Animal population structure under close inbreeding: the land snail *Rumina* in southern France. Amer. Natur. **110**:695–718.

Selander, R. K. and D. W. Kaufman. 1975. Genetic structure of populations of the brown snail (*Helix aspersa*). I. Microgeographic variation. Evolution **29**:385–401.

Sneath, P. H. A. and R. R. Sokal. 1973. Numerical taxonomy. San Francisco, W. H. Freeman. 573 pp.

Soulé, M. 1976. Allozyme variation: its determinants in space and time. In: F. J. Ayala (ed.), Molecular Evolution. Sunderland, Mass. Sinauer Associates, pp. 60–77.

Vermeij, G. J. 1975. Marine faunal dominance and molluscan shell form. Evolution **28**:656–664.

Woodruff, D. S. 1975a. A new approach to the systematics and ecology of the genus *Cerion*. Malacol. Rev. **8** (1–2):128.

Woodruff, D. S. 1975b. Allozyme variation and genic heterozygosity in the Bahamian pulmonate snail *Cerion bendalli*. Malacol. Rev. **8**:47–55.

Woodruff, D. S. and S. J. Gould, in prep. Genetics and morphometrics of the interaction between two semispecies of *Cerion* (Pulmonata) on Abaco.

Woodruff, D. S. and J. Quensen, in preparation. Ecological correlation of shell form in the West Indian *Cerion* land snails.

Wright, S. 1946. Isolation by distance under diverse systems of mating. Genetics **31**:39–59.

Wright, S. 1965. The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution **19**:395–420.

Yom Tov, Y. 1971. Body temperature and light reflectance in two desert snails. Proc. Malac. Soc. Lond. **39**:319–326.

NOTE ADDED IN PROOF

Since the above study was completed, a quantitative system of identifying allozymes has been developed (Woodruff and Burgess, in preparation). In future papers, *Cerion* allozymes will be characterized by their mobilities (under specified conditions) relative to the mobility of analogous allozymes derived from *C. incanum*. *C. incanum* from the Florida Keys is an appropriate standard as it is genetically invariant throughout most of its range (Woodruff, D.S., 1978, Evolution and adaptive radiation of *Cerion*: a remarkably diverse group of West Indian land snails. Malacologia 17: 223–239). Allozymes described here as 6-Pgdh-1^{b}, Mdh-1^{b}, Mdh-2^{b}, Got-1^{b}, and Lap-1^{a} are identical in their mobility to those of *C. incanum* and henceforth will be designated with the superscript 1.00 rather than a letter. For example, 6-Pgdh-1^{b} will now be 6-Pgdh-$1^{1.00}$.

In the course of quantifying the relative mobility of various allozymes, an error was discovered in the scoring of the Est-2 system as reported above. While *C. abacoense* and *C. bendalli* share a common set of Est-2 alleles, the allozyme here reported as Est-2^{f} does not have the same mobility in its commonest form in each species. Est-2^{f}, the commonest allozyme of *C. abacoense* and the populations from the areas of interaction, is now correctly designated Est-$2^{1.00}$. Est-2^{f} of *C. ben-*

dalli, on the other hand, is now known to migrate a little further. (This common *C. bendalli* allele is also present, though rare, in *C. abacoense*. Thus it remains true that neither species has a unique allele.) Consequently, Table 13 and Fig. 14 are incorrect with respect to their allozyme frequencies and the calculated interspecific genetic distances are slight underestimates. This finding does not significantly change our overall conclusions. A corrected data set, together with three years' additional data from the zone of interaction, will be reported in Woodruff and Gould (in prep.).

APPENDIX: LIST OF LOCALITIES

Specimens described in this paper may be found in the Museum of Comparative Zoology, Harvard University. The authors' collection sites are described below. Grid references are to the Grand Bahama and Abaco (Bahamas 1: 25,000 series) map series prepared by the Directorate of Overseas Surveys. Localities are arranged geographically from west to east. More precise data are available from the authors.

Loc.	Grid Ref.	General Area
Grand Bahama—*C. bendalli*		
212	QV 7293 29382	near Freeport airport
211	QV 7324 29351	junction of E. Sunrise Hwy and Shearwater Dr., Lucaya.
208	QV 7435 29388	near Blair House on Barbary Beach rd.
204	QV 7423 29436	site in pine forest, Lucaya Estate.
207	QV 7589 29488	forest site, North Perimeter Parkway, 1.0 km N. of Queens Hwy.
209	QV 7454 28497	North Perimeter Parkway
205	QV 7532 29459	Queens Highway, 0.8 km E. of Grand Bahama Hwy junction.
202	QV 7703 29483	High Rock
199	QV 7834 29591	North Riding Point—site A.
200	QV 7831 29599	North Riding Point—site B.
201	QV 7871 29548	The Gap
Little Abaco—*C. bendalli*		
213	TE 2202 2980	north coast at Crown Haven.
214	TE 2286 29792	Wood Cay village
216	TE 2436 29779	Little Abaco end of causeway between Little Abaco and Great Abaco.
Great Abaco—*C. bendalli*		Great Abaco end of causeway between Little Abaco and Great Abaco.
217	TE 2437 29780	
218	TE 2497 29752	Great Abaco Highway, 0.3 km W. Cooperstown (Pongo Carpet site 9 in Gould et al. 1974).
224	TE 2502 29750	Cooperstown (Pongo Carpet site 7).
223	TE 2510 29741	4.85 km N. of Pongo Carpet (site 6)
222	TE 2511 29740	4.75 km N. of Pongo Carpet (site 5)
226	TE 2517 29733	3.8 km N. of Pongo Carpet (site 4)
220	TE 2528 29723	2.4 km N. of Pongo Carpet (site 3)
219	TE 2531 29721	2.1 km N. of Pongo Carpet (site 2)
316	TE 2543 29707	Pongo Carpet (site 1)
228	TE 2725 29524	Rock Bluff road, Treasure Cay.
229	TE 2716 29529	Beach Way, Treasure Cay.
230	TE 2704 29542	Treasure Cay rd., 1.8 km NW of Loc. 229.
231	TE 2694 29550	Junction Treasure Cay rd and Great Abaco Hwy.
233	TE 2707 29495	Great Abaco Hwy. 5.9 km S. of Loc. 231.
240	TE 2866 29404	Bustick Bight
241	TE 2872 29394	Great Abaco Hwy, 1.1 km SE. of Loc. 240.
247	TE 2970 29383	John Cash Point, Marsh Harbour.
246	TE 2927 29273	Fossil locality exposed in road cut.
243	TE 2945 29275	Snake Cay rd., W. of causeway to Tuggy Cay.
245	TE 2949 29275	Tuggy Cay
244	TE 2953 29274	Snake Cay

APPENDIX [continued]

Loc.	Grid Ref.	General Area
Great Abaco—area of interaction between *C. bendalli* and *C. abacoense*		
261	TE 2916 29105	Cherokee Sound jetty
260	TE 2909 29095	Casuarina Point road junction
501	TE 2907 29095	0.5 km N. of Rocky Point
308	TE 2904 29093	0.3 km N. of Rocky Point
307	TE 2902 29092	Rocky Point
306	TE 2900 29092	0.3 km S. of Rocky Point
310	TE 2893 29093	approx. 1.0 km W. of Rocky Point
309	TE 2888 29098	1.6 km W. of Rocky Point
305	TE 2893 29088	2.9 km N. of Loc. 259
304	TE 2882 29078	1.6 km N. of Loc. 259
311	TE 2874 29074	NW. corner of Bahama Palm Shores estates.
249	TE 2845 29059	Great Abaco Hwy., 8.5 km S. of Cherokee rd. junct.
253	TD 2812 28943	Chalk Sound jetty.
255	TD 2809 28931	Great Abaco Hwy., Crossing Rocks estate junct.
251	TD 2594 28783	Sandy Point.
Great Abaco—*C. abacoense*		
259	TE 2873 29066	Bahama Palm Shores estate gazebo.
520	TE 2856 29050	2.2 km S. of Loc. 259.
521	TE 2848 29046	3.0 km S. of Loc. 259.
254	TD 2818 28942	Crossing Rocks Bay track: east end.
257	TD 2816 28933	Crossing Rocks estate beach: north end.
252	TD 2815 28925	Crossing Rocks estate beach: south end.
250	TD 2813 28617	Hole-in-the-Wall lighthouse.